STIMULUS-HORMONE INTERACTION AND THE GAMOPRACTIC BEHAVIOR OF THE MALE SYRIAN GOLDEN HAMSTER

By

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CHAPTER I

INTRODUCTION

Throughout its relatively brief history as a science, comparative psychology has utilized the concept of the phylogenetic continuity of behavior as its fundamental working hypothesis. During the century which has elapsed since Darwin first published his theory of evolution, interest in verification of the continuity hypothesis has ebbed and flowed. After an ambitious initial attempt, marked by the investigation of representatives from each of the major phyla, comparative psychologists narrowed the focus of their attention to a handful of species, predominantly from the class Mammalia. From within the literature of the past two decades, however, a trend has emerged which indicates both a reawakening of interest in, and recognition of the necessity for, species comparison (Schneirla, 1952). The problems posed by a "comparative" approach are, indeed, formidable. Perhaps one of the most difficult is that of describing and classifying the components of a given activity with the degree of scope and precision sufficient to insure valid inter-specific comparisons.

Gamopractic[1] activity should provide one of the more reliable

[1]The term "gamopractic," introduced by Dr. W. C. Dilger of Cornell University, denotes the broad spectrum of activities which constitute sexual behavior, and is unique in the sense that equal emphasis is placed upon the "appetitive" (pre-copulatory), as well as "consummatory" (copulatory) aspects of reproduction.

indices of phylogenetic continuity since it is universally present among living organisms. Unfortunately, however, the analysis of sexual behavior, in terms of inter-species similarities and dissimilarities, has been blocked (even among vertebrates) by adherence to the notion that below the level of primates sexual behavior is largely a function of the action of testicular hormones on specialized tissues. The most formal conceptualization of this position has been set forth by F. A. Beach (1942a).

Four factors are central to Beach's theory of the sexual behavior of male mammals. These include neural mechanisms which mediate erotic arousal (AM), other neural mechanisms responsible for execution of the coital act (CM), gonadal hormones, and special forms of external stimulation resulting in arousal (Beach, 1958). The occurrence of complete copulatory activity is dependent upon the effects of gonadal hormones and external stimulation, which combine to raise sexual arousal above the threshold level necessary to trigger consummatory activity which is executed by the CM. In males of the class Mammalia the AM has both cortical and subcortical representation. The influence of gonadal hormones upon sexual behavior is probably restricted to the subcortical level and lower portions of the brain and cord. The nature of the effect is a reduction in the threshold to stimulation. Cortical portions of the AM serve to supplement or augment the action of sex hormones upon lower centers in terms of the organization of individual experience, i.e., learning.

Presumably, then, the evolutionary increase in experiential control of sexual activities is an outcome of the increasing importance of the neocortex as a mediating agent. In addition, the partial

relaxation of hormonal dominance over sexual responsiveness makes possible greater latitude in individual sexual adjustments (Nissen, 1953). A relatively small cortical factor, on the other hand, as in male rodents and lagomorphs, permits a very limited modification of arousal through experience, so that susceptibility to sexual arousal and the capacity to mate are heavily dependent upon secretory activity of the reproductive glands.

This position is supported, in the main, by evidence which indicates that in "lower" mammals (rodents and lagomorphs), sexual behavior drops off rapidly after castration (Beach, 1948), whereas in primates and man the complete sexual pattern may last for months or even years (Bingham, 1928; Clark, 1945). Further, extra-sexual stimuli, previous sexual experiences, and social situations are much more important factors in initiating sexual activity in primates than in other mammals (Nissen, 1953; Hamilton, 1914).

Until recently this interpretation survived the test of "adequate explanation." Survival, however, appeared to have been a function of the kinds of hypotheses generated and the small number of species and methods used to test these hypotheses. That is, Beach has relied heavily upon data provided by the copulatory behavior of the male rat. The method developed to record the behavior of this species is restricted to the "consummatory" aspects of sexual behavior, i.e., mounts, intromissions, and ejaculations (Beach and Holz, 1946). On the other hand, the bulk of information regarding the mating behavior of "higher" mammals (carnivores, primates, and humans) has consisted largely of observations of the full range of behaviors (both courtship and copulation) in semi-controlled situations (Beach, 1958). The net

result is that observations derived by the use of these dissimilar methods have failed to provide any clear-cut steps between the two mammalian orders of rodents and primates. The evidence points instead to an abrupt transition in the complexity of erotic behaviors, and by implication, the factors which underlie them. It is possible, however, that the scoring system (method) developed for rodents has exerted a masking effect upon a pattern of reproductive behavior which would have otherwise provided for a smooth progression in the direction of increasing complexity.

Within the past few years there has been an accumulation of data militating against the interpretation of reproductive behavior of lower mammals as a unitary whole, governed predominantly by gonadal hormones. The two lines of evidence which are especially pertinent deal in turn with, (1) the development of a new method of observation and analysis of sexual behavior, and (2) the influence of experiential factors upon the sexual behavior of lower mammals.

In a comprehensive review of the literature, Aronson (1959) questions the efficacy of conceptualizing reproductive behavior in terms of a single, well-circumscribed entity such as "sex drive," or "level of sexual arousal." While he agrees with Beach's concept of an excitatory apparatus in the forebrain that is directly affected by gonadal hormones, he feels that the weight of evidence demands that this neuro-hormonal mechanism be considered only one, and possibly not the most significant, part of the total organization of sexual behavior. Further, he holds that the influence of experiential factors, at all phyletic levels, must be more carefully assessed.

Aronson (1959) suggests that implementation of this approach

requires a methodology of sufficient scope and flexibility to include observation of both the appetitive and consummatory components of the mating behavior of the species in question. A more accurate and useful description of gamopractic behavior can be obtained by reducing the total behavior pattern to the elements of which it is comprised. On the basis of this information it would be possible to state the precise relationship holding between neocortex, testicular hormones, and the various "bits" of behavior which go to make up the total sequence, both within and across species.

The method of experimentation most appropriate to this approach consists of two stages. The first is a broad, but detailed description of the mating behavior of the species under observation. Special attention is directed to the identification of those aspects of the pattern whose temporal proximity and qualitative similarity designate them as unique classes within the total sequence. Such data would provide a baseline or norm against which the effects of various experimental conditions could be evaluated. The second stage involves an analysis of the frequency of occurrence of these unique classes of behavior under conditions of experimental manipulation. Castration followed by replacement therapy is suggested as the means best suited for demonstrating the functional relationship holding between elements of overt behavior and testicular hormones.

The utility of this approach has already been shown by observations of vertebrates (ranging from fish to primates) which evidence the fact that among sexually experienced males, (1) castration affects the organization of the components of mating behavior more than its continued performance, (2) although some elements are more affected

than others, there is a great inter- and intra-species variability, and, finally, (3) that some elements of the pattern may even show an increase in frequency following castration (Aronson, 1959). For example, when males of an oviparous species of fish (Bathygobius soporator) were castrated they became nondiscriminatory and courted males, gravid, and nongravid females in like manner. The vigorous fanning movements of courtship declined, while characteristic gasping and snapping movements were more frequent than in intact controls. Behavior patterns associated with spawning (e.g., darkening, nest-rubbing, erection of genital papilla, and fertilization movements) were similar to those in intact fish (Tavolga, 1955). Clark, Aronson, and Gordon (1954) report essentially the same results following castration in the male platyfish, a viviparous form. In this case, however, the duration and persistency of various elements were observed to be highly variable among individuals. Studies by Rosenblatt and Aronson (1958a, 1958b) indicate that castration of sexually experienced male cats produces highly variable behavioral effects, which can be divided into three groups with respect to the retention and eventual decline of sexual responses. In type A animals, intromissions lasted for many months or even years, whereas the capacity for mounting continued almost indefinitely. In type B males, capacity for intromissions lasted for about two months, but very brief mounts without intromissions increased in frequency and continued for a year or more. In type C animals, intromissions dropped out rapidly, whereas mounting was weak and sporadic and rapidly disappeared.

In view of this kind of evidence, Aronson (1959) concludes that although alterations in the level of gonadal hormones undoubtedly cause

changes in central nervous processes, and may account for decreases or increases in the copulatory thresholds, changes in other systems and experiential factors must not be overlooked. A conspicuous feature of the studies reviewed above is the post-castration retention of some elements of mating behavior by sexually experienced males of species with limited cortical representation. This evidence leads to an increase in attention to the possible influences exerted by external stimuli on mating behavior in lower mammals.

A number of recent investigations have directed attention to the effect of experience by demonstrating that the cessation of sexual responses, which signifies satiation, is generally delayed when the male guinea pig (Grunt and Young, 1952a), rat (Tower and Whalen, 1961; Fisher, 1962), bull (Almquist and Hale, 1956), and monkey (Carpenter, 1942) are presented with a new stimulus female. Most important to the present inquiry are the studies which indicate the considerable response of lower mammals to external stimuli.

In a study designed to reveal the effect of stimulus variation on the sexual capacity of the male rat, Fisher (1962) found, (1) that following satiation with one female, a male's performance could be dramatically reinstated by the introduction of new females, and (2) that the addition of visual and auditory stimuli also produces a significant increase in capacity. In the analysis of his results Fisher states that "tests minimizing stimulus variation probably do not measure sexual capacity or generalized sexual satiation, but reflect adaptation to particular stimulus conditions" (p. 620). It would seem that by expanding the definition of satiation to include factors of stimulus adaptation, Fisher has given support to Aronson's (1959) contention that

even in species with limited cortical representation, sexual behavior is not wholly dependent upon the action of androgenic hormones. That is, the fact that testicular hormones were present cannot account for the increase in capacity, since that increase appeared only under conditions of stimulus change.

Fisher's (1962) study presents several interesting avenues of approach to the study of sexual behavior. First, and common to the investigation of any species, is the problem of determining the generality of increased sexual capacity following stimulus variation, and the nature of the response which is reactivated. Secondly, stimulus variation presents a very feasible method of determining the strength of those elements of sexual behavior which are not directly dependent upon the presence of gonadal hormones, that is, the frequency of those components of mating behavior displayed by the gonadectomized male when presented with successive receptive females.

A primary objective of this study was to determine the frequency of occurrence of those elements of behavior which constitute the gamopractic activity of the intact, sexually experienced, male hamster. This information was obtained by conducting tests to sexual exhaustion under two conditions: (1) repeated presentations of a single receptive female (stimulus stability), and (2) presentations of successive receptive females (stimulus variation). This data should provide the information necessary for later inter-specific comparisons involving the hamster.

A second goal of this study was an attempt to clarify the relationship between testicular hormones and elements of sexual behavior in a species representative of lower mammals. This was achieved by

exposing two groups of castrated hamsters, one of which underwent testosterone replacement therapy, to the experimental conditions described above.

Further, it was hoped that the responses of gonadectomized males to successive females would provide specification of at least one of the factors (external stimuli) responsible for the continued appearance of some aspects of mating behavior. That is, the method of stimulus variation should have provided a measure of the strength of responses occurring in the absence of endogenous hormones.

The golden hamster (Cricetus auratus) was well fitted to serve as the subject of this investigation for several reasons. First, the male hamster had been shown to exhibit a high level of well-defined sexual activity (Beach and Rabedeau, 1959). The recording of pertinent data thus proceeded with relative ease. Secondly, the hamster occupies a comparatively low phyletic position within the class Mammalia. It therefore provided information directly relevant to the problems cited above, namely, the somewhat obscure relationship between testicular hormones and erotic behavior in lower mammals. Lastly, being a rodent, the hamster was a most logical candidate for an extension of Fisher's (1962) work on the effect of stimulus variation in the rat.

Restatement of Problems

This investigation has been designed to answer the following questions: (1) what are the component acts which constitute the total sequence of sexual behavior in the male hamster; (2) what changes, if any, occur in the frequency of these components under conditions of stimulus variation; and (3) what relationship obtains between the various elements of sexual behavior and testicular hormones?

The first question, pertaining to the composition of reproductive behavior in the male hamster, can be answered by an analysis of the data obtained from observations of the Intact males. This descriptive evidence is considered a prerequisite to future inter- and intra-specific comparative work.

The effect of external stimuli on a species of lower mammal can be assessed by comparing the frequency of components of mating behavior of Normal males under conditions of stimulus variation and stimulus stability. An increase in the frequency of total components under the condition of stimulus variation would indicate the relative independence of the effect of experiential factors (external stimuli) from the effects of gonadal hormones.

Data relevant to the relationship between various elements of gamopractic activity and gonadal hormones can be obtained by comparisons of the responses of Castrates, Castrates with Hormone Replacement, and Normal males. A high degree of similarity in the frequency and patterning of responses shown by the Normal and Castrate with Replacement animals is assumed to indicate the functional equivalence of exogenous and endogenous hormones. Comparison of the Castrates and Castrates with Replacement should reveal both the qualitative and quantitative aspects of mating behavior whose expression is dependent upon the presence of gonadal hormones.

CHAPTER II

METHOD

Subjects

Thirty-five sexually naive male Syrian Golden hamsters, obtained from Manor Farms, New Jersey, constituted the experimental stock. They were 100-days of age at the outset of the study. Throughout the course of the experiment they were maintained on an ad libitum diet of purina lab chow and water. This diet was supplemented weekly with assorted cereal grains and vegetables. The animals were caged individually in an air-conditioned room in which a 12-hour light-dark cycle was maintained. The 40 ovariectomized females used in the sex testing were maintained in the same colony room under the conditions described above.

Apparatus

The preliminary testing was conducted in a converted aquarium which was divided into five compartments 12 1/2 inches in length and 8 inches in width. Lighting was provided by four 40-watt fluorescent tubes suspended 5 feet above the apparatus.

The apparatus for the experimental tests (shown in Figure 1) consisted of a clear plexiglass cylinder 12 inches high and 19 inches in diameter which rested upon a circular plate glass base. The platform was mounted in a circular opening in the top of a 24 x 24 x 24 inch parallelopiped. The parallelopiped was open at the front to allow

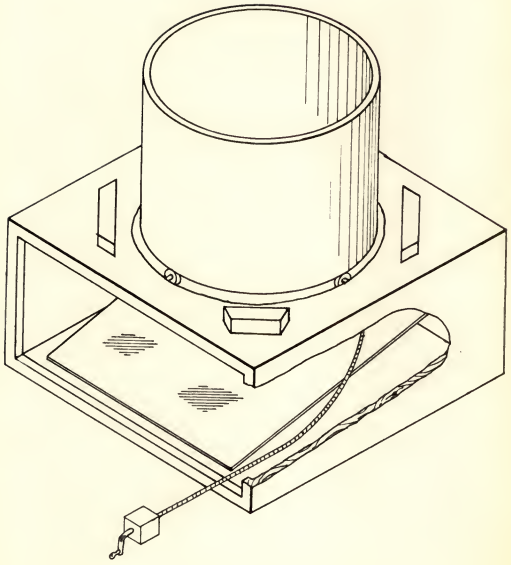

Fig. 1. Apparatus used in the experimental tests.

the observer to view up through the base of the platform by means of an 18 x 18 inch diagonal mirror. The mirror was adjustable to allow for various observation angles. This arrangement afforded both a ventral and a dorsal view of the subject. Rotation of the platform was made possible by a remote crank which changed the location of the subject relative to the observer. Variable-intensity, diffuse lighting was provided by three 25-watt bulbs embedded behind ground glass shields around the periphery of the platform. Maximum intensity (a total of 75 watts) was utilized throughout this study. A one-minute timer was used to activate a buzzer which divided total recording time into one-minute intervals. General room illumination was provided by four 40-watt fluorescent bulbs located approximately six feet above and five feet in front of the observation platform.

Procedure

Females. Forty ovariectomized female hamsters were used in the sex testing. Simulated estrus was induced by injection of .10 mg. estradiol (2.0 mg./cc in sesame oil) 75 hours before testing and 1.0 mg. progesterone (25 mg./cc in sesame oil) three hours before testing. Records were maintained throughout the study so that any changes in the test females' behavior and/or physical condition could be revealed and corrected if necessary (see Appendix A).

Pre-testing. In sessions spaced from seven to 11 days apart, each of the 35 experimental subjects was given four 30-minute periods of individual exposure to an estrus female. A male was placed in each of the aquarium compartments with an estrus female, so that five subjects were observed simultaneously. Intromission frequency was

recorded for each male. On the basis of their average number of intromissions during these tests, as shown in Table 1, 27 males were formed into nine subsets of matched trios. These averages appeared to be a stable basis for selection, since a Friedman two-way analysis of variance indicated no systematic changes in intromission frequency over the four tests (.05 level of confidence, $\underline{df} = 3$, $X^2 = 3.6$). Individual members of each trio were then assigned to one of three experimental groups: Castrates (C), Castrates with Hormone Replacement therapy (CR), and Normals (N). The remaining members of the experimental stock were designated as substitutes.

The length of time involved in a satiation test for an individual subject made it impossible to complete the tests for all members of the three groups in a single session. A further subdivision of groups was therefore carried out by which three animals from each of the experimental groups (C, CR, and N) were assigned to one of three replications. This procedure was chosen in order to distribute the possible effects of increasing age, and time since pre-testing, equally among the three groups. A replication, during which three animals from each of the three groups were tested, consumed approximately one month.

Surgery. All animals which had been assigned to groups C and CR underwent bilateral gonadectomies 45 days prior to their scheduled testing period. This amount of time has been found adequate for the completion of behavioral and physiological changes entailed by castration (Ortiz, 1953; Warren and Aronson, 1956; Kimmel, 1962). The operations were performed under sodium pentobarbital (nembutal) anesthetic; atropine sulfate was used to reduce respiratory complications. For those animals designated as CR's, hormone replacement therapy was

Table 1

Animal Assignments to Group and Replication According to Mean Frequency of Intromissions Achieved in Preliminary Testing*

	Castrates		Castrates with Replacement		Normals	
	Animal Number	Mean	Animal Number	Mean	Animal Number	Mean
Replication I	1	59.5	16	59.8	22	60.3
	7	38.5	14	37.8	32	36.5
	3	42.0	5	43.0	25	44.0
Replication II	9	49.0	24	49.2	11	49.3
	10	44.6	21	45.0	39	44.5
	8	47.8	19	48.0	18	46.5
Replication III	6	46.0	30	46.0	29	47.0
	28	41.3	34	41.0	37	40.5
	2	72.8	40	55.8	23	49.5

* Each row of three animals represents a matched trio.

initiated one week following surgery. Each CR received an intramuscular injection of 10 mg. perandren phenylacetate (50 mg./cc) once every 15 days throughout the duration of his particular test session. Perandren phenylacetate is a microcrystalline aqueous suspension of testosterone phenylacetate which has been shown to have a high degree of potency and lengthy duration of effect (Ciba Pharmaceutical Company, 1961). The remaining group of males (N) underwent the complete surgical procedure with the exception of the actual removal of the gonads.

Testing. All tests were conducted during the dark phase of the normal light-dark cycle, beginning no earlier than 9:30 PM. Time between tests for any given animal ranged from seven to 11 days to insure complete recovery from sexual exhaustion (Beach and Rabedeau, 1959). The testing schedule was arranged to accomplish the following: (1) a male was not exposed to a given female more than once throughout the entire study; (2) no female was used for "heavy" testing twice in succession (i.e., a Same condition or one of the first two females in a Fresh condition; explanations of these conditions appear below); (3) no male was consistently tested early or late in the experimental sessions. A sample schedule for one replication is shown in Appendix B. In the event that the scheduled female did not assume lordosis within five minutes of her introduction into the apparatus, she was removed to her home cage and the substitute was used in that test.

The components of sexual behavior which constituted the rating scale are listed and explained in Table 2. The observer typed the coded components as they occurred during the test sessions.

In order to familiarize the subjects with the test apparatus, they were allowed a 30-minute period of adaptation upon initial

Table 2

Sexual Behavior Rating Scale

Category of Behavior	Explanation	Code
Sniffing female		
Ano-genital region		sag
Body (other than ano-genital region)		sb
Licking female		
Ano-genital region		lag
Body (other than ano-genital region)		lb
Biting female		b
Pawing female		p
Mounting		
Posterior	Included both "mount" and "partial intromission" as defined by Beach and Rabedeau (1959)	mp
Abortive	Mount from the anterior or side of the female	ma
Intromission	Included both "complete intromission" and "ejaculation" as defined by Beach and Rabedeau (1959)	i
Sexual grooming	Licking self (ano-genital region)	sg

exposure. This period was reduced to five minutes on succeeding occasions.

Each male was tested twice under Same conditions and twice under Fresh conditions for a total of four tests. In a Same condition, each male was assigned one female and one substitute. In a given test, the male was removed from his cage and placed on the observation platform. Following the adaptation period, the female was removed from her home cage and placed with the male. Observed behaviors were recorded in succeeding one-minute intervals. When a period of 15 minutes had elapsed from the time of the last intromission, the female was removed from the apparatus and placed in a restraining cage. After one minute she was replaced into the apparatus with the male, who was again tested to a criterion of 15 minutes without intromission. This same procedure was repeated until there were two consecutive 15-minute periods without intromission (the criterion for satiation), at which time testing was terminated.

Under the Fresh condition, each male was assigned four females and one substitute. Each fresh female was an estrus female which had not been mated for a least seven days. Following his exposure period in the apparatus, the male's first scheduled female was removed from her home cage and placed with him. Recording continued until 15 minutes had elapsed since the last intromission. At this time the female was removed from the test apparatus and returned to her home cage. After an interval of one minute the second scheduled female was removed from her home cage and placed with the male. She remained with the male until 15 minutes without intromission had occurred. This procedure was repeated for the third and fourth fresh females. Due to the limited

number of available females, each male was alloted a total of only four females in a Fresh condition. Of these four, the number of females he actually received depended upon how early during the test he reached the criterion for satiation (two consecutive 15-minute periods without intromission).

Within each of the three replications the conditions were counter-balanced such that the order of testing for four males was Same-Fresh-Same-Fresh, while the remaining five males underwent order Fresh-Same-Fresh-Same.

CHAPTER III

RESULTS

Preliminary Analyses

Effect of Varying Intervals between Replications

Since three members of each of the three experimental groups were tested in each replication, it was desirable to determine whether or not the amount of time elapsing between the three replications (each of which consumed approximately 40 days) had any differential effect upon performance. A Kruskal-Wallis one-way analysis of variance was used to compare the total scores of the subjects in the three replications; no differences were found to exist (.05 level of confidence; $df = 2$, $H = .2$).

Handling of Incomplete Data

For the purpose of the statistical analyses in this study, the data of each animal consisted of averages of the scores from the two Same tests and averages of the scores from the two Fresh tests, or one set of mean scores for each of the two conditions. Several subjects, however, appeared ill on one of the nights during which they were scheduled to be tested. In such cases (see Appendix C), a single set of scores provided the data for that animal in one condition instead of the usual set of averages. Each animal was tested, however, at least once in each condition.

Description and Analyses of Gamopractic Behavior

Inter-group Comparisons

The summaries of the individual animals' behavior over the four occasions of measurement are presented in Appendix C. For the purposes of this analysis, the subdivisions within each of the categories of licking, sniffing, and mounting have been combined.

Figure 2 illustrates the mean frequency and standard deviation of each of the major components of sexual behavior by group. A comparison of the three groups on each category by a Kruskal-Wallis one-way analysis of variance indicated that they differed on licking (.05 level of confidence; $df = 2$; $H = 13.3$), mounting (.05 level of confidence; $df = 2$; $H = 17.3$), intromissions (.05 level confidence; $df = 2$; $H = 10.7$), and sexual grooming (.05 level of confidence; $df = 2$; $H = 15.0$). A Mann-Whitney U test showed that in all of the above mentioned categories the C's performed at a lower level than either the CR's or the N's. This result, however, is biased by the fact that while the CR's and N's average 116 minutes per test, the C's averaged only 47.5. The difference in time spent with the female (presumably a factor limiting the number of components of sexual behavior exhibited) can be accounted for by noting that the criterion of satiation involved two consecutive 15-minute periods without intromission, and the majority of C's failed to achieve intromission.

The behavior of the C group can be better assessed, therefore, by reference to Table 3, which shows the percentage distribution of total components over the various recorded categories. The C's showed no dramatic departure from the pattern shown by the N's and CR's.

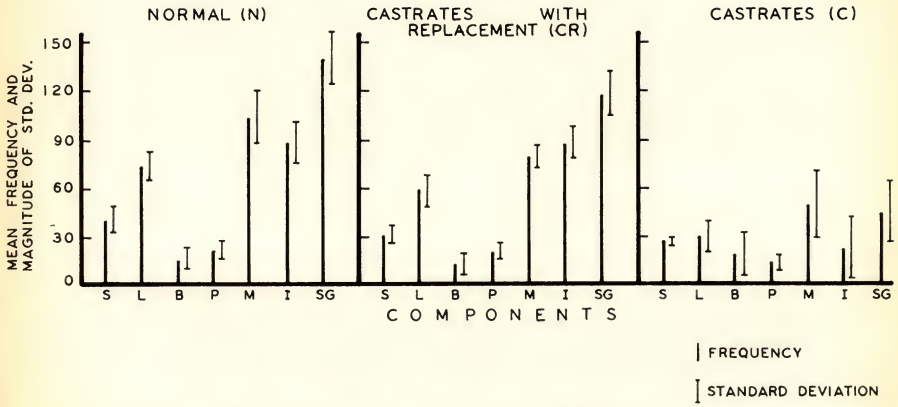

Fig. 2. The mean frequency and standard deviation of each behavioral component by group.

Table 3

The Percentage of Total Components Occurring in each Behavioral Category by Group

	Percentages						
	Sniffing	Licking	Biting	Pawing	Mounts	Intromissions	Sexual Grooming
Normals	8	16	2	4	22	18	30
Castrates with Replacement	8	14	2	4	21	21	30
Castrates	12	14	9	5	27	11	22

Intra-group Analyses

Normals and Castrates with Replacement. Since these two groups did not differ with respect to the average frequency of occurrence of components of sexual behavior, their results will be presented together. As shown in Figure 2, both the N's and CR's displayed their highest level of activity in the consummatory aspects of reproductive behavior. Similarly, the intra-group variation is relatively lower in the categories of mounting, intromissions, and sexual grooming. The considerable variance shown by both groups in the categories of biting and pawing would seem to be attributable to the fact that the rate at which these responses were emitted were peculiar to individual males (refer to Appendix C). The similarity between these two groups is also apparent in Table 3, in which the individual components are shown as percentages of the total scores.

A finding of considerable interest for both the CR's and N's was the "extended" intromission. The modal duration of a single "regular" intromission was from approximately 1.0 to 1.5 seconds. The "extended" intromission, however, was observed to average 8.2 seconds and constituted 28 percent of the total number of intromissions. It consistently appeared toward the latter part of a given test, following an average number of 54 regular intromissions. After a male had begun to make extended intromissions, it was highly unlikely that those of shorter duration would reappear.

Qualitatively, the typical sequence of sexual behavior for the N's and CR's involved, in the order of appearance, sniffing, licking, and in some instances, biting and pawing, followed by a number of mounts and/or intromissions which alternated with sexual grooming.

This complete sequence was typically followed by an extended period of sexual and general grooming. Toward the end of a given test the male often engaged in short periods of exploration before reinstigating the sequence of sexual behaviors. A further observation was that as a test progressed over time, the male became more distractable, i.e., less attentive to the female; in addition, the duration of appetitive behavior within a given sequence tended to increase. No bizzare behaviors such as continuous biting were observed to occur among the N's and CR's.

Castrates. The most striking aspect of the Cs' behavior was their intra-group variability, apparent in terms of the magnitude of the standard deviations in Figure 2. This variability was attributed to relatively stable individual differences in post-castration gamopractic activity. Figure 3, for example, illustrates the mean frequency for three males who are provisionally labelled "types" Castrate-A (C-A), Castrate-B (C-B), and Castrate-C (C-C). These three animals ranked 1.0, 4.5, and 9.0, respectively, in the C group on the mean number of total components over the four experimental tests. The type C-A male continued over four occasions of measurement (up to 80 days after castration) to achieve a high frequency of intromissions. The type C-B male made very few intromissions, but displayed a relatively high number of mounts and sexual grooming. The sexual responsiveness of the type C-C animal was considerably depressed over all categories.

Qualitatively, several bizzare bits of behavior were noted among the C group, such as the persistent and continuous biting shown by male number 10 on one occasion. Such occurrences, however, were infrequent and did not appear to characterize individuals. Generally, the

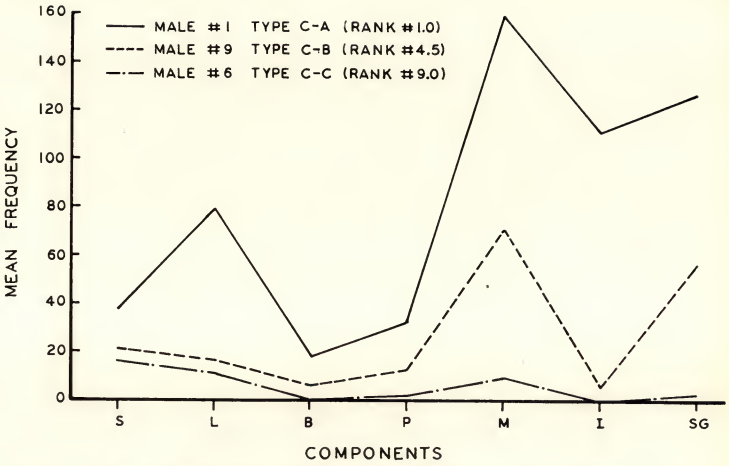

Fig. 3. The mean frequency of each behavioral component for three "types" of castrated animals.

organization of the typical sequence of the Cs' behavior did not vary markedly from that of the other two groups. Differences which were noted seemed to occur with respect to the intensity of sexual responses, the C's appearing more distractable than the CR's and N's. The C, for example, was quite likely to interrupt short sequences of gamopractic activity with exploration, and was much less susceptible to the solicitations of the female. In addition, the duration of appetitive activities such as sniffing, licking, pawing, and biting, normally occurring prior to mounting and/or intromissions within a given sequence, appeared to be considerably extended for the C's.

Comparison of Fresh and Same Conditions

Preliminary Analyses

Before an analysis of any differential effects of the Fresh and Same conditions could be made, it was necessary to ascertain the comparability of the subjects undergoing the ordering Same-Fresh-Same-Fresh with those undergoing the ordering Fresh-Same-Fresh-Same. When the scores of the animals in the two orders were compared by a Mann-Whitney U test for the N and CR groups, it was apparent that the order of conditions had no effect upon total performance (.05 level of confidence; $N = 9$; $U = 25$) or upon intromission frequency (.05 level of confidence; $N = 9$; $U = 23$).

Since the first female in both the Fresh and Same conditions was "new" to the male, it was also necessary to determine whether any differences in total intromission frequency under the two conditions were due to a differential number of responses made with the first female (or during the first presentation of a female). A Wilcoxin signed-ranks

test for N's and CR's indicated that there was no difference between the two conditions in the number of intromissions exhibited with the first female (or presentation) (.05 level of confidence; $N = 18$; $T = 49.5$).

Normals and Castrates with Replacement

A Wilcoxin sign-test of the effects of stimulus stability versus stimulus variation (Figure 4) showed that the average total performance was significantly higher in the Fresh condition for both the CR's (.05 level of confidence; $N = 9$; $T = 3$) and the N's (.05 level of confidence; $N = 9$; $T = 2$). The similarity between the two groups was indicated by a Mann-Whitney U test which showed no difference between the two groups' total performances in either the Fresh (.05 level of confidence; $N = 9$; $U = 30$) or the Same (.05 level of confidence; $N = 9$, $U = 20$) condition. Likewise, when analysed in terms of intromission frequency the two groups showed remarkable similarity under both the Fresh (.05 level of confidence; $N = 9$; $U = 30$) and the Same (.05 level of confidence; $N = 9$; $U = 28$) conditions.

The distribution of total components over categories in the Fresh and Same conditions for each group is shown in Figure 5. In the Fresh condition there was a general increase in frequency for all components; for the N's and CR's the amount of increase is, however, in all cases proportionate to the frequency in the Same condition. In the combined CR and N group it was observed that there were three animals (numbers 30, 24, and 29) which did not show an increase in terms of total components in the Fresh condition, and one animal (number 34) which did not show an increase in intromission frequency in the Fresh condition.

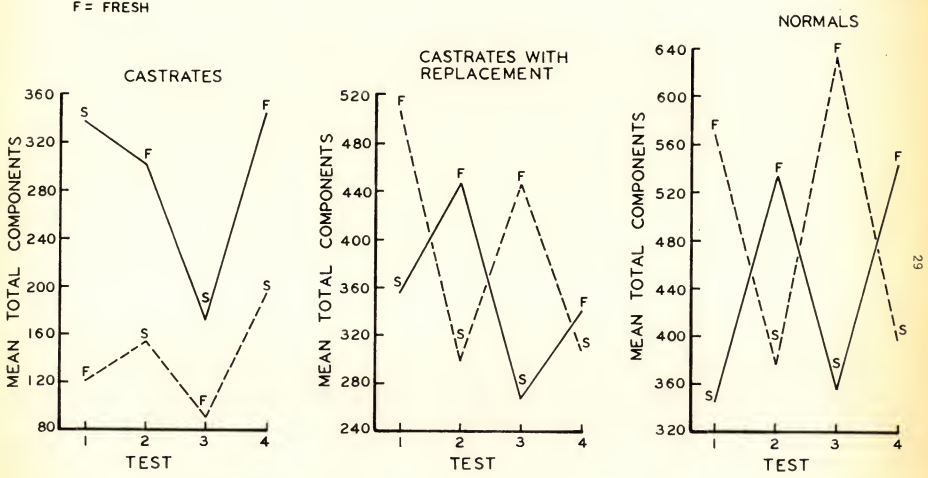

Fig. 4. The mean frequency of total components under Same and Fresh conditions by group.

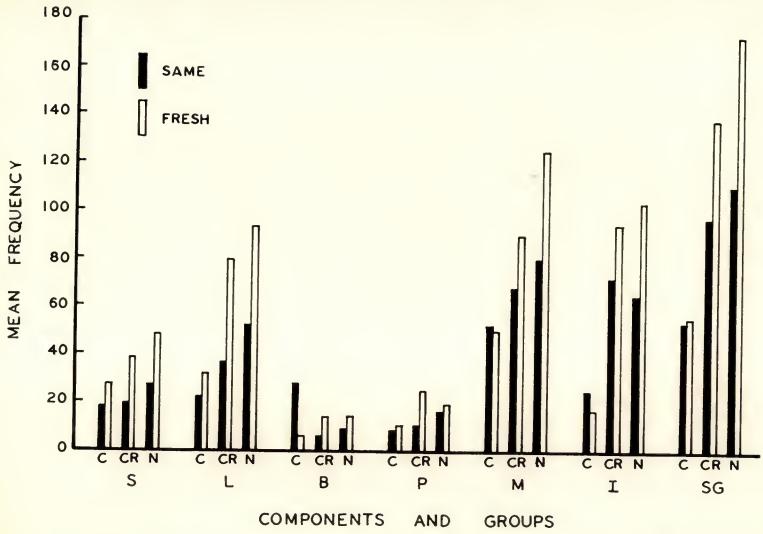

Fig. 5. The mean frequency of each behavioral component under Same and Fresh conditions by group.

Figure 6 is presented in order to show the percentage distribution of total components over categories of response for each group. Once again there is a striking resemblance between the N's and CR's in the general composition of sexual behavior, with both showing a slightly higher percentage of consummatory activity (mounting, intromissions, and sexual grooming) in the Same condition.

Responses to succeeding females in the Fresh condition and repeated exposures to the same female in the Same condition are shown in terms of average frequency of responses and percentages in Tables 4 through 6. Of some interest is the increase in frequency shown by the N's and CR's with females 2, 3, and 4 in the Fresh condition. When the composition of behavior for the two groups was compared, it was noted that although there was considerable similarity, the N's did tend toward a higher proportion of activities with females 2, 3, and 4 in both the Same and the Fresh conditions than the CR's.

While the N's and CR's did not differ with respect to their performances under the Fresh and Same conditions, there appeared to be considerable individual variation within groups. The N and CR groups were, therefore, combined and the members were placed in a "high" or "low" group depending upon whether their total number of intromissions exceeded 300. This division yielded two groups of nine subjects each, with the high group having 1894 intromissions in the Fresh condition and 1210 in the Same condition, while the low group had 1330 in the Fresh condition and 1088 in the Same. The difference between the Fresh and Same scores of the high group was compared with the difference between the Fresh and Same scores for the low group by a Mann-Whitney U test. The difference for the high group was significantly greater

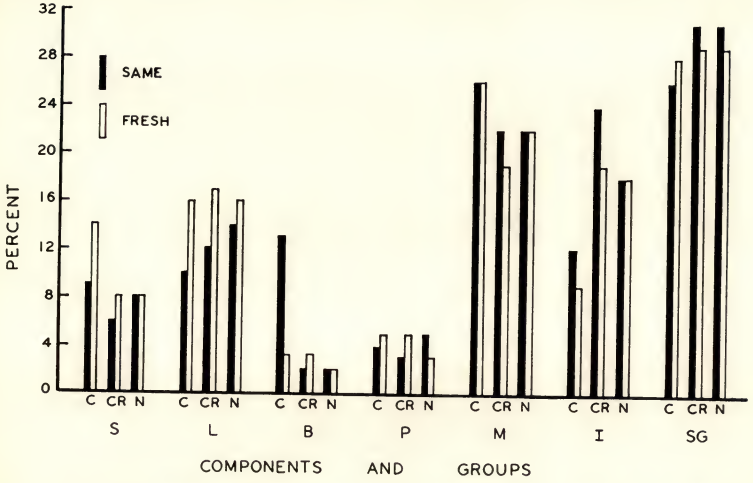

Fig. 6. The percentage of total components in each behavioral category under Same and Fresh conditions by group.

Table 4

Average Frequencies and Percentages of Responses to Succeeding Females in the Fresh Condition and Repeated Exposures to the Same Female in the Same Condition for the Normal Group

		Components							
		S	L	B	P	M	I	SG	Total
Same Condition									
Presentation 1	f	21	45	8	12	66	61	95	308
	percent	75	86	89	73	83	95	86	86
Presentation 2	f	5	6	1	3	11	3	12	41
	percent	18	11	11	17	14	5	11	11
Presentation 3	f	2	1	0	2	2	0	3	10
	percent	7	3	0	10	3	0	3	3
Presentation 4	f								
	percent								
Fresh Condition									
Female 1	f	22	46	8	8	81	71	107	343
	percent	46	51	56	41	65	69	64	60
Female 2	f	13	25	4	5	25	21	36	129
	percent	27	27	25	24	20	20	22	23
Female 3	f	8	13	2	4	13	8	16	64
	percent	17	14	12	21	10	7	9	11
Female 4	f	5	7	1	3	6	4	9	35
	percent	10	8	7	14	5	4	5	6

Table 5

Average Frequencies and Percentages of Responses to Succeeding Females in the Fresh Condition and Repeated Exposures to the Same Female in the Same Condition for the Castrate with Replacement Group

		Components							
		S	L	B	P	M	I	SG	Total
Same Condition									
Presentation 1	f	15	34	5	8	62	71	90	285
	percent	80	92	100	80	91	97	94	93
Presentation 2	f	3	2	0	2	5	2	5	19
	percent	15	5	0	20	8	3	5	6
Presentation 3	f	1	1	0	0	1	0	1	4
	percent	5	3	0	0	1	0	1	1
Presentation 4	f								
	percent								
Fresh Condition									
Female 1	f	22	45	3	14	66	73	103	326
	percent	55	57	23	54	73	78	74	68
Female 2	f	11	19	9	7	15	13	22	96
	percent	27	24	69	27	16	14	16	20
Female 3	f	5	11	1	4	6	5	9	41
	percent	12	14	8	15	7	6	7	9
Female 4	f	2	4	0	1	3	2	4	16
	percent	6	5	0	4	4	2	3	3

Table 6

Average Frequencies and Percentages of Responses to Succeeding Females in the Fresh Condition and Repeated Exposures to the Same Female in the Same Condition for the Castrate Group

		Components							
		S	L	B	P	M	I	SG	Total
Same Condition									
Presentation 1	f	13	17	15	6	36	16	33	136
	percent	72	80	55	75	67	62	60	65
Presentation 2	f	5	3	12	2	14	4	14	54
	percent	28	15	42	25	26	14	26	25
Presentation 3	f	0	1	1	0	4	5	7	19
	percent	0	5	3	0	7	21	12	9
Presentation 4	f	0	0	0	0	0	1	1	2
	percent	0	0	0	0	0	3	2	1
Fresh Condition									
Female 1	f	15	18	4	6	34	11	27	115
	percent	56	57	80	60	66	64	49	58
Female 2	f	9	8	1	3	12	3	21	57
	percent	34	27	20	30	23	19	38	29
Female 3	f	1	3	0	1	4	2	5	16
	percent	6	10	0	10	8	11	9	9
Female 4	f	1	2	0	0	2	1	2	8
	percent	4	6	0	0	3	6	4	4

than that for the low group ($p = .05$; $N = 9$; $U = 16$). These results indicated that the high group was more responsive to successive females in the Fresh condition than the low group.

Castrates

When analyzed by a Wilcoxin signed-ranks test the total performance scores for the C group were found to be independent of conditions (.05 level of confidence; $N = 9$; $T = 22$). For this reason the C's were not included in the analyses for order and first female effect. In spite of the fact that there were no systematic responses to conditions, reference to Figure 4 indicates that the C group did show some increase in response under Fresh conditions in the categories of sniffing, licking, and pawing, relatively no change in mounting and sexual grooming, and a decrease in intromissions. The probable cause of any lack of clear-cut response to conditions lies in the variability of the group, i.e., five C's showed increases in total components in the Fresh condition, while the remaining four had higher scores in the Same condition. For example, under the ordering Same-Fresh-Same-Fresh, the type C-A animal cited above (Description and Analyses of Gamopractic Behavior: Castrates) had total component frequencies of 440, 665, 318, and 822; the type C-B animal scored 438, 90, 153, and 80; while the type C-C male scored 20, 51, 36, and 58.

When the patterning of behavior is considered (Figure 5), the C group shows about the same distribution as the other two groups, even exceeding CR's and N's in percentage of mounting and sniffing. As pointed out earlier, the high percentage of biting is attributable to the performance of one male (number 10) on one occasion.

When responses to succeeding females are examined, no overall

differences in pattern can be seen (Table 6). That is, the distribution of components for the C group is approximately proportional over females. When comparisons are made over groups, however, it appears that the C's showed a considerable increase with females 2, 3, and 4 in the Same condition as opposed to the CR's and N's. A further difference between the three groups is the lack of a general increase in either frequency or proportion shown by the C group when Fresh and Same conditions are compared.

CHAPTER IV

DISCUSSION

An Overview

The purpose of the present study was to obtain a detailed description of the gamopractic behavior of the Normal, Castrate with Hormone Replacement, and Castrate male hamster under conditions of stimulus variation and stability. The results of inter- and intra-group comparisons and their relation to relevant empirical evidence and theoretical positions are presented in the following order.

1. The method devised to measure and classify the gamopractic behavior of the male hamster is discussed in terms of its adequacy and compared to similar devices developed and used in studies of rodent behavior.

2. A primary goal of this study was to obtain a description of the frequency and distribution of the elements which constitute the reproductive behavior of the Intact male hamster. The results indicated that Normal males displayed their highest level of activity in the consummatory aspects of behavior with considerable intra-group variability in both appetitive and consummatory responses. This variability is considered in terms of the experiential and genetic factors which have been shown to influence it.

3. A second problem underlying this investigation concerned the effect of external stimuli upon the sexual responses of a representative

species of lower mammals. Intact male hamsters were found to respond to conditions of stimulus variation with a systematic increase in response frequency. This evidence is compared with similar findings in other vertebrate species. Several suggestions are made for studies designed to investigate both the perceptual and neurological factors underlying changes in response relative to stimulus conditions. The significance of these results, which indicate the influence of experiential factors on the sexual behavior of lower mammals, is then considered with respect to the theoretical positions of Beach (1958) and Aronson (1959), while sexual satiation, as seen in the Intact male hamster, is related to Thorpe's (1958) notion of "experimental extinction."

4. The final concern of this project was the nature of the relation holding between the various elements of gamopractic activity and testicular hormones. This problem had two ramifications. The first of these was related to data bearing on the functional equivalence of exogenous and endogenous hormones, which were obtained by comparing the frequency and distribution of responses exhibited by Intact males and Castrates with Hormone Replacement. Analysis indicated that there was a statistical similarity between the two groups. This similarity is discussed with particular emphasis on the trend toward a depressed frequency of responses shown by the CR's under both Fresh and Same conditions. Explanations for the existance of this trend are couched in terms of the matching procedures used to form the two groups and the fact that a uniform dosage level was administered to the CR subjects. The second aspect of the problem regarding gonadal hormones and sexual responses involved specification of changes in the frequency and

organization of components following gonadectomy, i.e., in the absence of testicular hormones. When the Castrates were compared with the CR's and N's it was found that although they exhibited a lower frequency of components, there was no apparent change in the organization of reproductive behavior.

It was concluded that the qualitative aspects of behavior in the male hamster are not dependent upon gonadal hormones, while the quantitative aspects undergo a considerable decline. These findings are related to the bulk of evidence which indicates that among male vertebrates both organization and frequency of sexual responses undergo changes following castration. Suggestions are made which might provide for reconciliation of the data from male hamsters with those which are generally found among vertebrates.

The most significant finding with respect to the post-castration behavior of hamsters was the extreme individual variation in the maintenance of gamopractic activity. The emergence of individuals with sustained post-operative potency is compared to related findings among higher mammals and it is concluded that, relative to average life span, the behavior of the hamster parallels that of carnivores. This finding is discussed in terms of the theoretical position of Beach (1958), and several suggestions are made with regard to clarification of the behavioral characteristics of "types" of male hamsters.

The Castrates were also found to exhibit individual differences in response to the Same and Fresh conditions, with a trend toward increased responses in the Same condition. This is discussed in terms of the qualitative observation that, in general, the Castrated male hamsters' reaction to the stimulus female tends toward one or the other extreme

on the "arousal" continuum. It is suggested that these characteristic levels of arousal are under the influence of genetic factors.

Measurement and Classification of Behavior

A primary objective of this study was to obtain a complete description of the gamopractic behavior of the male hamster. The procedure developed to accomplish this was based upon the selection of all of the aspects of reproductive activity which, by their temporal proximity and qualitative similarity, could be designated as unique classes of behavior. The components, given in the order in which they appear in the course of sexual interaction, are sniffing, licking, biting, pawing, mounting, intromissions, and sexual self-grooming. This scale was found to be fully adequate to describe the activities of the subjects during the experimental tests, and to compare and contrast the three groups of subjects.

The general specifications for this scale were based upon Aronson's (1959) suggestion that all of the elements of reproductive behavior must be considered before it is possible to delineate the relationship between these elements and the mechanisms presumed to underlie them. Unfortunately, neither of the scoring systems most prevalent in this country (Young, 1961) were suitable. The scale which has reached its final form through the efforts of Beach and Holz (1946) is primarily concerned with the copulatory responses of the male rat. Young and Grunt (1951), on the other hand, have developed a much broader descriptive device for recording both the pre-copulatory and copulatory responses of the male guinea pig.

Both of these systems include "ejaculation" as a discreet and identifiable response, although Beach and Holz (1946) specify that in

the male rat "ejaculation" refers solely to observable mating reactions, without implications as to the discharge of seminal fluid. The inclusion of this component tends to reduce the possible number of species comparisons, since in the present study the male hamster was not observed to exhibit any discreet response pattern which could be reliably identified as "ejaculation." Further, it is felt that the degree of importance attached to such a response is questionable in view of Chang and Shaeffer's (1957) study of ejaculation in the male hamster. They conclude that "although the insertion of the penis may be observed at copulation, whether he will ejaculate at each copulation is not known" (p. 107). It is felt, however, that there is need for a careful investigation of the correspondence between the behavioral and physiological characteristics of ejaculation in the male hamster.

Gamopractic Behavior of the Normal Male Hamster

"Appetitive" and "consumatory" behavior. A major purpose of this study was to obtain a description of the occurrence of the individual elements which constitute the gamopractic behavior of the intact, sexually experienced male hamster. When the results were analyzed in terms of the percentage of total components occurring in each category of behavior (Table 3, page 23), the average distribution for the Normal male was as follows: sniffing, 8 percent; licking 16 percent; biting, 2 percent; pawing, 4 percent; mounts, 22 percent; intromissions, 18 percent; and sexual grooming, 30 percent.

Discussions of sexual behavior often make reference to a duality of functions, first noted by Craig (1918), and later given prominence by Beach (1958) and Soulairac (1952a, 1952b, 1952c). Craig (1918) applied the term "appetitive" to those aspects of mating behavior which

lead the animal toward the external situation necessary to copulation. "Appetitive" behaviors were characteristically more variable in form than the rigid and stereotyped "consummatory" components, which constitute the final acts in the sequence. When the gamopractic behavior of the male hamster was placed in this frame of reference, the activities of sniffing, licking, biting, and pawing were designated as "appetitive," while mounting, intromission, and sexual grooming constituted the "consummatory" phase. This is essentially the same dichotomy which Young (1961) has described for the rat and guinea pig, although for these species 'ejaculation"is included as the major constituent of the consummatory act.

Analysis of the distribution of the male hamster's activity in terms of the above mentioned dichotomy indicates that approximately 30 percent of the behaviors shown are appetitive, while 70 percent are consummatory (Table 3, page 23). These percentages are probably not representative of the behavior of this species in their natural environment. This speculation is based primarily upon the experimental procedures employed here to insure the selection of completely receptive stimulus females. It is most probable that under uncontrolled conditions the male hamster would encounter a less selected population of stimulus females and could, therefore, display a higher proportion of approach and courtship behaviors.

When the various categories of response within the two major divisions are compared, marked differences in the Normal subjects' intra-group variability become apparent in the appetitive behaviors, particularly biting and pawing (Figure 2, page 22). The frequency with which these activities occurred seemed to be characteristic of given

animals, although some degree of variation was seen throughout the group. Less pronounced individual differences were apparent in consummatory behavior.

These findings were not unexpected. Craig (1918) observed that appetitive behavior is typically more variable than consummatory behavior. With regard to the differences between individuals of a species, Young (1961) noted that "in the guinea pig and rat they are manifested by variations in the elements of the pattern and by variation in the scores . . . and these [variations] tend to persist" (p. 1179). The same tendency toward individual differences in both the patterning and frequency of elements of sexual behavior has been noted in the hamster (Beach and Pauker, 1949), chickens (Wood-Gush and Osborne, 1956), cats (Green, Clemente and De Grcot, 1957), and chimpanzees (Young and Orbison, 1944).

A considerable amount of research has been devoted to discovery of the factors responsible for the observed intra- and inter-specific differences in both appetitive and consummatory behavior. It has been established that differential behavior patterns in the rat (Beach and Holz-Tucker, 1949) and guinea pig (Grunt and Young, 1952b) are not due to individual differences in the amount of exogenous or endogenous testicular hormones (Soulairac, 1950).[1] The evidence, therefore, points to the "conclusion that the character of the behavior induced by gonadal hormones is determined in large part by the nature of the soma or substrate (all of the tissues mediating sexual behavior) on which the

[1]While individual differences do persist at a constant dosage level, there is some evidence which indicates that castrated male rats may require differential amounts of exogenous hormones in order to achieve response scores which are quantitatively comparable to their own pre-operative level (Beach and Fowler, 1959).

hormones act" (Young, 1961, p. 1213). In accord with these findings, investigations have been focused upon the factors which exert a direct effect on the substrate and, thus, an indirect effect upon sexual behavior.

In a review of the genetic basis for individual, strain, and species variation in sexual behavior, Goy and Jakway (1962) conclude that the evidence indicates that among invertebrates, fish, birds, and lower mammals, (1) genetic variance accounts largely for variation in the quantitative aspects of components, and (2) that the genetic mechanisms determining the quantitative expression of various components are relatively independent; i.e., genetic manipulations have been reported which affect only one component of the sexual behavior of male animals. These authors also note, however, that "some phenotypic variation exists within genetically identical groups even though experimenters adhere to rigid standards in rearing and in observations" (p. 102). These latter observations direct attention to another variable which is known to mediate individual expressions of gamopractic behavior.

Experience, afforded by contact with other animals, has been shown to be a second major factor influencing the soma (Young, 1961). Studies of the male guinea pig (Valenstein, Riss, and Young, 1955), rat (Zimbardo, 1958), and cat (Rosenblatt and Aronson, 1958a, 1958b) indicate that variation in the degree of "social" experience is sharply reflected in the pattern of sexual behavior exhibited by individual males of these species. Since this is a relatively new area of investigation there are several problems with respect to the influence of experiential factors on individual differences in the expression of quantitative components of sexual behavior. Young (1961) has observed

the need for identification of, (1) the effective element or elements afforded by experience with other animals, (2) the relationship between age, experience, and sexual behavior, (3) the interaction between level of gonadal hormones and experience, and (4) the locus of action, i.e., whether experience affects the appetitive mechanism, the consummatory mechanism, or both.

The information provided by the genetic and experiential studies presented above is sufficient to provide a general explanation of the individual differences observed among the Intact male hamsters in this study. Hopefully, investigation of the problems in each of these areas will serve to further clarify the variables which shape these individual differences.

Fresh and Same conditions. Analysis of the effect of external stimuli upon the mating behavior of male hamsters contains implications relevant to both empirical and theoretical problems. The empirical problem is essentially concerned with the specification of external variables which have comparable effects on the behavior of various species. The theoretical problem involves the degree to which the reproductive behavior of lower mammals can be affected by experience.

Stimulus variation has been shown to re-instigate a vigorous response in sexually satiated male rats (Tower and Whalen, 1961; Fisher, 1962), guinea pigs (Grunt and Young, 1952a), bulls (Almquist and Hale, 1956), and monkeys (Carpenter, 1942). The effect has been noted to be quite general for the members of these experimental populations; the reinstated response is described as similar in form to that displayed under conditions of stimulus stability (Young, 1961). Such extra-sexual stimuli as diffuse sound and light have also been

found sufficient to restore some degree of response in the satiated male rat (Fisher, 1962). Similar responses to extra-sexual stimuli have been observed in the bull (Almquist and Hale, 1956).

The typical procedure has been to allow the male to mate with a given stimulus female until he has reached sexual satiation, i.e., ceased to make sexual responses. Under conditions of stimulus stability the female was then removed from the experimental apparatus and almost immediately reintroduced into it. This procedure was continued until reintroduction of the same female ceased to elicit sexual responses from the male. Under conditions of stimulus variation the same procedure held, except that satiation with a given female was followed by the removal of that female and the subsequent introduction of a fresh female. In the present study, stimulus variation has been denoted as the Fresh condition, while stimulus stability was entitled the Same condition.

The response of the Intact male hamster to the condition of stimulus variation (Fresh condition) in this study was a dramatic reinstatement of gamopractic activity. This is shown in Figure 5 (page 30) as an increase in the frequency over all the categories of behavior except biting. Further, the form (in terms of the percentage distribution of total components) of the reinstated response, was very similar to that shown under conditions of stimulus stability (Same condition) (Figure 6, page 32). Inspection of the percent of component acts exhibited with succeeding females indicates that the general pattern of response did not change, although the frequency of total components declined (Table 4, page 33). It appears, therefore, that the male hamster executes very nearly the same sequences of behavior with succeeding

(Fresh) females as with the Same female.

A comparison between the rat (Fisher, 1962) and the hamster suggests that the rat is somewhat more responsive to female change. The intact, adult, male rat evidenceda 100 percent increase in intromission frequency in the Fresh condition as compared with the 63 percent increase shown by the male hamster. Unfortunately, the two studies lack sufficient similarity in design to provide for further comparisons. It should be pointed out, however, that investigation of the effect of extra-sexual stimuli should be carried out for the hamster in order to provide additional information regarding similarities or differences between these two species of rodents.

The evidence provided by the Intact male hamster leads quite naturally to speculations regarding the exact nature of the stimulus which calls forth the extended patterns of response. Superficial appraisal suggests that the male hamster was capable of recognizing individual stimulus females, i.e., was able to differentiate between succeeding stimuli to the extent that re-exposures to the same female were responded to in a different manner than presentations of fresh females. This conclusion is still tentative, however, since it is entirely possible that the male hamster's response was determined by the presence (with the same female) or absence (with the fresh female) of stimuli which had arisen from his own previous interaction with the female.

Further work in this area would be of value in delineating the perceptual capacity of a species with limited neocortical representation. Without complimentary neuro-physiological investigation, however, it would be difficult to determine whether the relatively small amount of

neocortex present in lower mammals is sufficient to mediate such response changes, or whether the mechanisms involved in the translation of external stimuli into response patterns are subcortical.

Some evidence regarding cortical function and the sexual behavior of rodents has been accumulated. Observations of the copulatory behavior of partially decorticated rats (Beach, 1940, 1944) revealed that there was a decrease (proportional to the magnitude of the lesion) in the percentage of tests in which copulatory behavior occurred, but that the number of copulations during each positive test was not affected. Beach concluded that cortical lesions reduce the responsiveness of the male rat, thus reducing the effect of stimuli which have previously elicited sexual arousal. Stamm has pointed to the importance of median cortical tissue for the expression of such basic behavior patterns as hoarding (1953, 1954) and maternal behavior (1955) in the rat. In an extension of Stamm's work, Friel (1963) found that median cortical lesions in the male hamster were followed by a reduced number of intromissions.

Two conclusions can be drawn from this evidence. First, large cortical lesions (20 to 75 percent) in any location disrupt behavior patterns such as sexual activity, maternal behavior, and hoarding. Smaller lesions (less than 20 percent), localized in the median cortex, can effect a comparable disruption. Secondly, the individual components comprising these activities (e.g., the act of copulation) seem to be left intact, but the arousal and/or total sequencing of these components appears to be disturbed.

It appears, therefore, that while the neocortex is involved in the mediation of external stimuli and complex responses, normal function

of the median cortex is of equal, if not greater, importance to the execution of sequential patterns of behavior among rodents. A more complete evaluation of the functional relation between these neural mechanisms and the components of sexual behavior could be obtained by conducting satiation tests under conditions of stimulus stability and variation. This suggestion seems fruitful, since, (1) tests to sexual exhaustion would provide a sufficient duration for anomalous behaviors to appear, and (2) the effect of Same and Fresh conditions would provide a sound method for assessing the effort of cortical ablation upon responsiveness to external stimuli.

As stated above, the theoretical problem relating to conditions of stimulus variation and stability involves the degree to which the reproductive behavior of lower mammals can be affected by experience, i.e., external stimuli. Beach (1958) holds that among "these animals (lagomorphs and rodents), the susceptibility to sexual arousal and the capacity to mate are heavily dependent upon the secretory activity of the reproductive glands," and that ". . . experiential control of sexual activity is an outcome of the increasing importance of the neocortex as a mediating agent, . . ." (pp. 275 and 278).

The considerable increase in frequency of responses shown by rats (Fisher, 1962), guinea pigs (Grunt and Young, 1952a), and hamsters (present study) under conditions of stimulus variation casts some doubt upon the general application of this interpretation. That is, the increase in gamopractic activity in response to Fresh conditions must have been due to "experiential control" since there was no reason to suspect changes in the "secretory activity of the reproductive glands." Thus, the evidence is taken to indicate that the behavior of organisms

without benefit of extensive encephalization is indeed influenced by external stimuli and that this influence functions independent of changes in the level of gonadal hormones.

These findings point to the value of the approach taken by Aronson (1959) who has re-emphasized the need for careful assessment of the effects of experiential factors at all phyletic levels. The data from the present study tend to support his general thesis that mating behavior in lower forms is not exclusively dependent upon testicular hormones and that there is a smooth phyletic progression in the complexity of underlying mechanisms. Hopefully, subsequent investigations of the part-processes involved in expressions of sexual behavior will lead to a much better insight into evolutionary trends.

The data involving the behavior of male hamsters under conditions of stimulus stability and variation also provide a basis for suggestions regarding the mechanisms underlying the decline and eventual cessation of sexual activity within a single test. Thorpe (1958) has suggested that "experimental extinction" includes three factors: (1) "competition" or "interference," (2) a decrease in "response specific motivation," and (3) a decrease in "stimulus specific motivation" (habituation). Fatigue, which is assumed to represent Thorpe's "competition" or "interference" factor, was indicated by the appearance of the extended intromission (defined in Results section: Intra-group observations). The degree of "response specific motivation" is inferred from the proportionate amounts of time which a male spent in sexual activity as opposed to general exploration of the apparatus. The "stimulus specific" factor is assumed to correspond with the changes in the male's behavior relative to the same and fresh females.

With regard to the ordering and interaction of these factors, the extended intromission generally appeared first within a given test, followed by an increase in exploratory activity and general distractibility. The fatigue factor, manifested by the extended intromissions, was not subject to change due to stimulus conditions. The response specific factor, exploratory activity and general distractibility, however, showed differential amounts of change in responses to stimulus conditions. Under stimulus stability, the removal and replacement of the same female was sufficient in most cases to instigate a slight renewal of sexual activity. The response was meager, however, in comparison with that which followed the introduction of a fresh female. Apparently the introduction of a new stimulus object was sufficient to partially overrule the effects of decreasing response specific motivation and increasing fatigue. As noted by the decreasing number of components displayed with succeeding females in the Fresh condition (Tables 4 and 5, pages 33 and 34, respectively), however, the effect of stimulus change was only partial.

Gamopractic Behavior of the Castrated Male Hamster with Hormone Replacement Therapy

Castration followed by hormone replacement therapy has been suggested by Aronson (1959) as the means best suited for demonstrating the functional relationship between elements of overt behavior and testicular hormones. This proposition appears to be based upon the tacit assumption that the effect of exogenous hormones on castrates is functionally equivalent to the effect of endogenous testicular hormones on intact males. Comparisons of the Castrate with Replacement (CR) and the Normal (N) male hamsters in the present study gave statistical

support to this assumption.[2]

Appetitive and consummatory behavior. Considerable similarity was shown between the CR and N males in terms of the frequency with which the various components of gamopractic behavior were displayed (Figure 2, page 22). This resemblance was also evident in the percentage distribution of total components across the categories of sexual behavior (Table 3, page 23), where the CR's exhibited the following pattern: sniffing, 8 percent; licking, 14 percent; biting, 2 percent; pawing, 4 percent; mounts, 21 percent; intromission, 21 percent; and sexual grooming, 22 percent. When these data were placed in Craig's (1918) classification, 28 percent of the responses were appetitive while 72 percent were consummatory. These results closely parallel the same dichotomy shown the Intact males (30 percent appetitive and 70 percent consummatory). The relative amount of intragroup variability in appetitive as contrasted to consummatory behavior also closely resembles that of the N group (Figure 2, page 22).

Fresh and Same conditions. The CRs' response to stimulus variation (Fresh condition) was a statistically significant increase in the total number of components which were exhibited (Figure 4, page 29). No differences were shown to exist between the CR's and N's either in terms of the increase in total components or the increase in intromission frequency in the Fresh condition (Results section: Intragroup observations). Of some interest, however, is the fact that the CR's evidenced a 27 percent increase in intromissions in the Fresh condition, which was considerably less than the 63 percent increase of

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[2]Because of the similarity between these two groups, several topics in the above discussion of the sexual responses of the Intact male are equally applicable in the Castrate with Replacement group.

the N group (Tables 4 and 5, pages 33 and 34, respectively).

The results of statistical analyses would justify the conclusion that hormone replacement therapy fully restores the castrated male hamster's ability to execute normal patterns of gamopractic behavior. Certain trends, however, make such a conclusion premature. These include, (1) the tendency for the CRs' mean frequency of response to be generally lower than the Ns', (2) the relatively depressed response of the CR's to the condition of stimulus variation, and (3) the observation that three of the nine CR's failed to show any frequency change in response to the experimental conditions.

There are at least two explanations for these discrepancies. The first involves the adequacy of the procedures which were used to form the CR and N groups. It is conceivable that the individual differences which became manifest in the experimental tests (mean duration, 116 minutes) were not revealed by the 30-minute preliminary tests, so that by chance the CR and N groups were never wholly comparable. Secondly, the uniform dosage level of androgens which was administered to the CR group may not have been sufficient to restore the full capacities of all subjects. Evidence implicating individual differences in the amount of exogenous hormone necessary to restore preoperative sexual vigor is somewhat divided and may, in fact, reflect species differences. In a study of the effects of different concentrations of androgen on sexual behavior in the castrated male rat, Beach and Fowler (1959) concluded that the hormone requirements of individual rats do vary. When castrated male guinea pigs are treated with a constant amount of testosterone proportionate, on the other hand, they return to the level of sexual responsiveness exhibited prior to castration (Grunt and

Young, 1953). Any conclusions regarding the tendency toward reduced responsiveness of the CR's must await empirical investigations of these problems.

Gamopractic Behavior of the Castrated Male Hamster

Considerable controversy exists with regard to the relative degree of influence exerted by experience and by testicular hormones on the reproductive activities of lower mammals. Observation of the gamopractic behavior of sexually experienced, gonadectomized males was suggested as a method by which to obtain information pertinent to the solution of this problem.

On the basis of a comprehensive review of evidence gained by this method, Aronson (1959) has concluded that among sexually experienced male vertebrates, castration, (1) has a greater effect upon the organization of sexual behavior than upon its duration, (2) may be followed by an increase in frequency of some elements in the pattern, and (3) may affect some elements of the pattern more than others, although there is great inter- and intra-specific variability. Further, experiential factors are assumed to exert an effect upon species at all points along the phyletic scale.

Beach (1958), on the other hand, has consistently maintained that the degree of influence dependent upon previous sexual experience is negligible with regard to the post-castration behavior of lower mammals. This is based upon evidence which indicates that within a few weeks of gonadectomy the sexual responses of male rodents have suffered a sharp decline. He concludes, therefore, that "the relatively small cortical factor as in the male rodent . . . cannot support normal copulatory behavior in the absense of sex hormones" (p. 281).

The results of the Castrate group offer considerable evidence regarding the relationship between testicular hormones and the organization of gamopractic behavior in the male hamster, a species representative of lower mammals. In general, the C group showed a lower frequency of the components of sexual behavior than the N's and CR's, although, as pointed out earlier, this result was biased by the length of time the Castrates remained in the apparatus as compared with the CR's and N's (Figure 2, page 22).

The percentage distribution of components over categories was therefore considered, and it appeared that the average Castrate was following a pattern which was in most respects very similar to the average Intact male. The only apparent difference was that relative to the other two groups, the C's evidenced a higher percentage of mounts and a lower percentage of intromissions. Clarification of this difference required that mounts and intromissions be regarded as a single response. This grouping was felt to be justified in that a mount can easily be viewed as an unsuccessful intromission, while an intromission represents a successful mount. When the percentages of responses in the categories of mounts and intromissions are combined, the N's are found to have a total of 40 percent, the CR's, 42 percent, and the C's, 38 percent. It would appear, therefore, that the C group was exhibiting the same degree of consummatory sexual activity as the Intact and Hormone Replacement subjects, but were incapable of achieving a proportionate number of intromissions. The relatively lower percentage of sexual grooming for this group can be accounted for by the qualitative observation that this response regularly followed intromissions, while occurring less often after mounts. The most general

effect of castration in this study appears to have been a decline in the frequency of all elements of reproductive activity, with a reduction in the percentage of intromissions.

On the basis of these findings it is evident that in the male hamster post-castration sexual behavior does not conform in all details to the conclusions which Aronson (1959) has drawn from observations of species throughout the vertebrate phyla. More specifically, there were no differences between the Castrates and the Normal males in the organization of the percentage distribution of the components of gamopractic behavior (other than the greater mount/intromission ratio explained above). Qualitative assessment of the C's indicated no noticeable changes in the order of appearance of the elements of mating behavior within a given sequence. Similarly, no general increases in the frequency of single elements of gamopractic behavior were observed to occur. On the other hand, individual differences in sexual vigor constituted the most prominent feature of the C group. (This topic will be more fully discussed later.)

There are at least two explanations for the disparity between post-castration behavioral changes observed in the hamster in this study and the bulk of evidence supporting Aronson's (1959) conclusions. First, it would be worthwhile to study the post-castration behavior of the male hamster over a greater length of time, since up to 80 days after castration several males were continuing to achieve a high frequency of intromissions. It is probable that the full physiological and/or psychological effects of gonadectomy on behavior had not materialized within the time alloted. Secondly, the amount of time which the average C spent with the female was limited, in the present study, by

the "satiation" criterion which was defined as 15 minutes without intromission. As noted in the Results section, relatively few Castrates achieved successful intromission. It is possible, therefore, that the time limits enforced within a given test were too stringent to allow for aberrations in the organization and frequency of individual elements. There would be considerable value in a design in which the duration of an individual male's exposure to the stimulus female was alloted on the basis of that male's pre-castration performance.

Probably the most interesting fact to emerge from observations of the C group was the difference among individuals in post-operative sexual capacity. "Types" of Castrates (Figure 3, page 26) were distinguished which paralled those found among cats (Rosenblatt and Aronson, 1958a) and dogs (Schwartz and Beach, 1954). Existence of the type C-A male (of which there were two in the group of nine Castrates) indicates that even among lower mammals, there are individuals whose sustained sexual capacities are comparable to both carnivores and primates.

Minimization of individual differences in the duration of post-castration potency in rodents is probably due to the tendency to compare species in terms of absolute rather than relative time. For example, the life span of male cats and dogs is approximately 12 years, while the median upper limit for the male hamster is approximately 20 months (Pailey, 1950). The ability of some experienced, adult, male cats and dogs to retain potency for two years after castration is hardly more significant than the performance of some experienced, adult, male hamsters who were observed to achieve a high proportion of intromissions three months after castration (Bunnell, B. N., and Flesher, Carol, in preparation).

These data are assumed to support Aronson's (1959) contention that effects of experience are comparable among higher and lower mammals.

This is quite a different conclusion from that expressed by Beach (1958). On the basis of evidence that "rodents and lagomorphs reach a prepuberal level within a few weeks after operation . . . while some male dogs show no such change for more than two years postoperatively," he concludes "that the phylogenetic differences between carnivores and rodents include a partial reduction in the degree to which masculine sexual behavior depends upon testicular hormones" (p. 275). Such an assumption appears tenuous when the duration of post-castration potency is considered relative to the life spans of the two species.

Although there is a large volume of research on sexual behavior, the number of investigations reporting on the discovery and specification of types of castrates is quite limited (Young, 1961). Some indirect evidence can be found, however, which points to the behavioral characteristics of types and, in addition, to the mechanisms presumed to underly them. There is, for example, the generally accepted finding that castration depresses mating tendencies least in the most vigorous copulators among rabbits (Stone, 1932), rats (Beach, 1948), hamsters (Beach and Pauker, 1949), cats (Rosenblatt and Aronson, 1958a), and dogs (Schwartz and Beach, 1954). This evidence is supported by the results of the present study, in that the two type C-A males ranked first and second in mean frequency of intromissions in pre-testing. Experience with the guinea pig, however, has indicated that the sexual responses of groups of high, medium, and low scoring males declined at the same rate following castration (Grunt and Young, 1953).

The importance of genetic and experiential factors in the shaping of individual differences has been discussed above with regard to the gamopractic behavior of the Intact male hamster. Although several studies in each of these areas have implications for the current topic, no directly applicable information was available. No doubt this is due to the recent recognition that types of male animals can be identified by their response to the withdrawal of gonadal hormones. Reference to the present study indicates a number of problems in this area.

Questions specific to the male hamster concern, (1) the probability of constructing a classification system for types, (2) identification of patterns and/or frequencies of elements of sexual behavior characteristic of given types, (3) duration of the C-A's response and changes over time, and (4) the development of a predictive device based upon preoperative sexual performance. A final problem concerns the degree of experience necessary to the development of specific types. In their work with the cat, Rosenblatt and Aronson (1958a, 1958b) have achieved partial solutions to questions 1 and 2 above, and have established that postoperative responses are dependent upon post-puberal sexual experience prior to gonadectomy.

Same and Fresh conditions. The method of stimulus variation was incorporated in the design of this study for the purpose of specifying one of the factors (external stimuli) responsible for the continued appearance of gamopractic behaviors in the absence of gonadal hormones. If the Castrates had responded uniformly to succeeding females with a relative increase in the frequency of components, the method might also have provided a measure of the strength of those

responses. As shown in Figure 4 (page 29), however, the Castrates failed to exhibit a systematic response to changes in stimulus conditions.

Close inspection of Table 6 (page 35) indicates a slight increase in the mean frequency of total components and intromissions in the Same condition. The most unique feature of the C group (as compared with the CR's and N's) was the relatively high frequency of responses to the second, third, and fourth presentations of the female in the Same condition. The most probable explanation of those results rests upon the qualitative observation that the individual males' reactions to the female characteristically tended toward one or the other extreme of "arousal."

More specifically, it was observed that upon the introduction of the female, certain of the Castrates would exhibit a considerable amount of generalized activity, i.e., running and grooming alternating with short sequences of extremely disorganized mating behavior. Usually several minutes would elapse before the male displayed any sign of the typical pattern of gamopractic activity. Re-exposure to the same female in the Same condition did not call forth this disorganized response. In the Fresh condition, however, the male was presented with a new stimulus female after each 15-minute period without intromission. In most cases, the response to a new stimulus object re-initiated the intense, non-directed activity. Consequently, the pattern of running, grooming, and short disorganized sequences of reproductive activity occurred throughout the Fresh test.

Similar findings have been reported for the rat (Beach, 1942a, 1942b) and the guinea pig (Grunt, 1954). Grunt has concluded that the

most probable explanation is that this non-directed hyperexcitability is a reflection of frustration which yields a clear indication of cortical activity in the absence of androgenic stimulation. Young (1961) has suggested that "the effect of gonadal hormones on the central nervous tissue could be in the nature of a coordinating, integrating action rather than a matter of excitation" (p. 1208).

The behavior of Castrates on the other end of the "arousal" continuum was distinguished by an initial lack of response to the stimulus female. In this case, introduction of the female was usually followed by a short period of sniffing, after which the male returned to wandering about the apparatus. It was not unusual for the male to collide with, and occasionally walk over, the female. There was little indication of the specific factors which eventually elicited mating behavior. The typical patterning of the behavior of these males moved in the direction of an increasing frequency in the number of components exhibited per unit of time and was not noticeably affected by Same and Fresh conditions.

In general, the effects of these characteristic levels of "arousal" are, (1) a reduction in the frequency of sexual responses in the Fresh condition, which is due to the "hyperexcitable" Castrate, and (2) a relative depression in percent of responses to the first stimulus female in both Fresh and Same conditions, which is the result of "high arousal" in one case and "low arousal" in the other.

These qualitative observations indicate that the degree of arousal elicited by external stimuli, in the absense of gonadal hormones, is subject to considerable individual variation. As noted in the discussion of Intact males, "the character of behavior induced by gonadal

hormones is determined in large part by the nature of the soma or substrate (all tissues mediating sexual behavior) on which the hormones act" (Young, 1961, p. 1213). The substrate, in turn, is directly affected by genetic and experiential factors. It is suggested that the nature of the response to sexual stimuli, following withdrawal of gonadal hormones, is a reflection of the genetically determined sensitivity of the substrate. This seems most probable in view of the fact that sexual experience was controlled for the Castrates in this study. Such an explanation seems probable in view of the findings by Goy and Jakway (1962) that "genetic factors have been shown to be important in determining the limits of variability or plasticity of the sexual behavior within a species" (p. 109). Both the isolation of these factors and their specific effects await the results of further investigation.

General Conclusions

The methodological approach taken in this study was fruitful to the extent of providing a description of the gamopractic behavior of the hamster which is felt to be adequate to future inter- and intra-species comparisons. The results of the present investigation indicate considerable individual variation in both the quantitative and qualitative expressions of the elements of mating behavior. The above observation applies equally to Intact and Castrated subjects. It seems most probable that this variation can be attributed to specific genetic and experiential factors.

Considerable significance was attached to the evidence regarding the relative influence of experiential factors on the sexual behavior of hamsters. Both the increased frequency of sexual responses to stimulus variation exhibited by the intact males and the emergence of

types of Castrates are believed to support Aronson's suggestion that the dichotomy between higher and lower mammals is not so great as previously suspected. That is, the apparent independence of these behaviors from testicular hormones furnishes evidence of a more orderly progression in the complexity of factors mediating reproductive behavior from rodents to primates.

Several suggestions for future work have been made. Foremost among these is the need for specification of the experiential factors (including extra-sexual stimuli), and the genetic mechanisms which determine both inter- and intra-specific differences in mating behavior. Considerable emphasis has also been placed on the need for more information regarding the neurological and hormonal processes underlying this response pattern.

CHAPTER V

SUMMARY

The objectives of this study were, (1) to determine the frequency of occurrence of those elements of behavior which constitute the gamopractic activity of the intact, sexually experienced, male hamster, (2) to clarify the relationship between testicular hormones and elements of sexual behavior in a species representative of lower mammals, and (3) to specify the effects of stimulus variation upon the sexual behavior of the male hamster.

In order to achieve these goals, three groups of nine male hamsters, Normals (N), Castrates with Hormone Replacement Therapy (CR), and Castrates (C), were tested to sexual exhaustion twice under conditions of stimulus stability (repeated presentations of a single receptive female), and twice under conditions of stimulus variation (presentations of successive receptive females). Seven major components of sexual behavior were recorded: sniffing, licking, biting, pawing, mounting, intromissions, and sexual grooming.

Inter-group analyses showed that the CR's and N's did not differ with respect to the average frequency of occurrence of components of sexual behavior. Both groups displayed their highest level of activity in the consummatory (mounts, intromissions, and sexual grooming) aspects of behavior, with relatively more variability in the appetitive (sniffing, licking, pawing, and biting) components. Pronounced

individual differences were noted among the N's and CR's in both appetitive and consummatory behaviors. The Castrates performed at a significantly lower level than the CR's and N's on licking, mounting, intromissions, and sexual grooming. The distribution of responses across categories was, however, similar for the three groups. The typical sequence of mating behavior for all three groups consisted of sniffing, licking, and in some instances, biting and pawing of the female, followed by a number of mounts and/or intromissions which alternated with sexual grooming.

Intra-group analyses indicated that average total performances were significantly higher for both the CR's and N's under conditions of stimulus variation, but that the distribution of responses was similar in form to that shown under stimulus stability. The total performance scores for the Castrates evidenced no systematic change relative to the two stimulus conditions.

The description of gamopractic activity of the Intact male hamster was discussed relative to the variability shown in both the appetitive and consummatory aspects of behavior. This variability was, in turn, related to the genetic and experiential factors presumed to underly it. The relationship between testicular hormones and the qualitative and quantitative expressions of mating behavior were considered both in terms of, (1) the statistically significant functional equivalence of exogenous and endogenous hormones which was revealed by comparisons of the N and CR subjects, and (2) the extreme variation in sexual vigor shown by individual Castrates.

The increased frequency of responses shown by both the N and CR groups to conditions of stimulus variation was compared to similar

findings among other species. It was concluded that in the male N and CR hamsters, the effect of experiential factors (external stimuli) are independent of the effect of gonadal hormones.

The implications of the effect of experiential factors (response to stimulus variation and the sustained capacities shown by some Castrates) on a species of lower mammal were considered relative to the theoretical positions of Beach (1958) and Aronson (1959).

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APPENDICES

APPENDIX A

Example and Explanation of Female Record Sheets

Female _____

Date of usage	Date and Time of Injections		Male with which used	Number of minutes used	Comments
	Estr	Prog			

Females that were larger than the males were eliminated during pre-testing.

Information noted under "Comments":

Behavior toward the male: females which initiated fighting with the males during pretesting were eliminated.

Physical condition: two females were replaced during the course of testing due to viral infections.

APPENDIX B

Sample Testing Schedule

Arabic numbers = male designations
Letters = female designations

Replication I

SU	M	T	W	TH	F	SA
	SAME 22 5 1 32 A E I L B F J M	FRESH 14 3 7 P S W N T X Q U B^2 R V E^2 C D K	FRESH 16 25 G^2 N^2 F^2 L^2 H^2 M^2 J^2 K^2 O O^2			
				SAME 27 7 3 16 14 Q R P U V N S W T X	FRESH 22 5 B^2 B E^2 O^2 K^2 I L^2 L F Y	FRESH 32 1 M^2 H^2 N^2 J^2 A F^2 E G^2 J M
SAME 32 1 5 22 L^2 Y F^2 F E^2 O^2 J^2 N^2	FRESH 7 14 3 M S I A G^2 N B U Q P B^2 R C D K	FRESH 16 25 J T W F H X M^2 H^2 Z D^2				
			SAME 25 3 14 7 16 P F M^2 Q R E A B N L	FRESH 5 22 U V N^2 H^2 K S L^2 T J M	FRESH 1 32 B^2 J^2 E^2 O^2 W F^2 X G^2 Y I^2	

APPENDIX C

Summaries of Data for Individual Subjects

Male # 22 Group N Replication I

		sag	sb	Total	lag	lb	Total	b	p	ma	mp	i	ie	Total	sg	Total
First Same	1	2	5	7	24	1	25	0	0	1	53	29	0	29	79	194
	2	1	8	9	19	1	20	0	0	1	55	16	0	16	72	173
	3	1	1	2	2	0	2	0	0	0	1	0	0	0	2	7
	4															
	T	4	14	18	45	2	47	0	0	2	109	45	0	45	153	374
Sec. Same	1	6	21	18	22	3	25	1	1	1	54	40	14	54	82	236
	2	1	2	3	1	0	1	0	0	1	5	0	1	1	4	15
	3	1	1	2	2	0	2	0	0	0	0	0	0	0	0	4
	4															
	T	8	15	23	25	3	28	1	1	2	59	40	15	55	86	255
Same Ave.	1	4.0	8.5	12.5	23.0	2.0	25.0	0.5	0.5	1.0	53.5	34.5	7.0	41.5	80.5	215.0
	2	1.0	5.0	6.0	10.0	0.5	10.5	0.0	0.0	1.0	30.0	8.0	0.5	8.5	38.0	94.0
	3	1.0	1.0	2.0	2.0	0.0	2.0	0.0	0.0	0.0	0.5	0.0	0.0	0.0	1.0	5.5
	4															
	T	6.0	14.5	20.5	35.0	2.5	37.5	0.5	0.5	2.0	84.0	42.5	7.5	50.0	119.5	342.5
First Fresh	1	1	14	15	52	12	64	0	6	3	40	44	13	57	91	276
	2	2	12	14	31	14	45	1	3	2	14	7	24	31	50	160
	3	0	11	11	26	8	34	0	4	6	26	0	16	16	38	135
	4	1	5	6	23	3	26	0	3	1	20	0	11	11	22	89
	T	4	42	46	132	37	169	1	16	12	100	51	64	115	201	660
Sec. Fresh	1	4	4	8	20	2	22	0	1	13	17	40	24	64	93	218
	2	3	7	10	22	0	22	0	0	1	43	5	19	24	41	141
	3	4	1	5	22	1	23	0	0	7	31	3	32	35	49	150
	4	3	5	8	5	0	5	0	0	0	8	2	7	9	14	44
	T	14	17	31	69	3	72	0	1	21	99	50	82	132	197	553
Fresh Ave.	1	2.5	9.0	11.5	36.0	7.0	43.0	0.0	3.5	8.0	28.5	42.0	18.5	60.5	92.0	247.0
	2	2.5	9.5	12.0	26.5	7.0	33.5	0.5	1.5	1.5	28.5	6.0	21.5	27.5	45.5	150.5
	3	2.0	6.0	8.0	24.0	4.5	28.5	0.0	2.0	6.5	28.5	1.5	24.0	25.5	43.5	142.5
	4	2.0	5.0	7.0	14.0	1.5	15.5	0.0	1.5	0.5	14.0	1.0	9.0	10.0	18.0	66.5
	T	9.0	29.5	38.5	100.5	20.0	120.5	0.5	8.5	16.5	99.5	50.5	73.0	123.5	199.0	606.5

Male # 25 Group N Replication I

		sag	sb	Total	lag	lb	Total	b	p	ma	mp	i	ie	Total	sg	Total
First Same	1	2	28	30	37	21	58	21	14	0	20	39	30	69	92	304
	2	0	3	3	0	1	1	1	2	0	0	0	2	2	2	11
	3	1	5	6	1	2	3	1	2	0	0	0	0	0	0	14
	4															
	T	3	36	39	38	24	62	23	18	0	22	39	32	71	94	329
Sec. Same	1	6	37	43	64	8	72	27	23	0	32	37	32	69	93	359
	2	0	5	5	4	3	7	1	4	0	1	0	1	1	2	18
	3	0	3	3	1	1	2	0	1	0	1	0	0	0	1	8
	4															
	T	6	45	51	69	12	81	28	28	0	34	37	33	70	96	388
Same Ave.	1	4.0	32.5	36.5	50.5	14.5	65.0	24.0	18.5	0.0	26.0	38.0	31.0	69.0	92.5	331.5
	2	0.0	4.0	4.0	2.0	2.0	4.0	1.0	3.0	0.0	0.5	0.0	1.5	1.5	2.0	16.0
	3	0.5	4.0	4.5	1.0	1.5	2.5	0.5	1.5	0.0	1.5	0.0	0.0	0.0	0.5	11.0
	4															
	T	4.5	40.5	45.0	53.5	18.0	71.5	25.5	23.0	0.0	28.0	38.0	32.5	70.5	95.0	358.5
First Fresh	1	14	37	51	59	9	68	44	5	0	39	38	38	76	117	400
	2	12	12	24	31	3	34	17	0	0	11	0	14	14	29	129
	3	4	4	8	11	3	14	8	0	0	2	0	2	2	3	37
	4	4	3	7	16	0	16	5	1	0	2	0	8	8	9	48
	T	34	56	90	117	15	132	74	6	0	54	38	62	100	158	614
Sec. Fresh	1															
	2															
	3															
	4				Animal not tested due to illness.											
	T															
Fresh Ave.	1	14.0	37.0	51.0	59.0	9.0	68.0	44.0	5.0	0.0	39.0	38.0	38.0	76.0	117.0	400.0
	2	12.0	12.0	24.0	31.0	3.0	34.0	17.0	0.0	0.0	11.0	0.0	14.0	14.0	29.0	129.0
	3	4.0	4.0	8.0	11.0	3.0	14.0	8.0	0.0	0.0	2.0	0.0	2.0	2.0	3.0	37.0
	4	4.0	3.0	7.0	16.0	0.0	16.0	5.0	1.0	0.0	2.0	0.0	8.0	8.0	9.0	48.0
	T	34.0	56.0	90.0	117.0	15.0	132.0	74.0	6.0	0.0	54.0	38.0	62.0	100.0	158.0	614.0

Male # 32 Group N Replication I

		sag	sb	Total	lag	lb	Total	b	p	ma	mp	i	ie	Total	sg	Total
First Same	1	2	1	3	26	2	28	1	1	3	58	40	2	42	69	205
	2	0	1	1	0	1	1	0	0	0	1	0	0	0	2	5
	3															
	4															
	T	2	2	4	26	3	29	1	1	3	59	40	2	42	71	210
Sec. Same	1	4	10	14	31	1	32	1	22	0	28	36	9	45	60	202
	2	2	5	7	1	1	2	0	3	2	1	0	1	1	2	18
	3	0	1	1	0	1	1	0	1	0	0	0	0	0	1	4
	4															
	T	6	16	22	32	3	35	1	26	2	29	36	10	46	63	224
Same Ave.	1	3.0	5.5	8.5	28.5	1.5	30.0	1.0	11.5	1.5	43.0	38.0	5.5	43.5	64.5	203.5
	2	1.0	3.0	4.0	0.5	1.0	1.5	0.0	1.5	1.0	1.0	0.0	0.5	0.5	2.0	11.5
	3	0.0	0.5	0.5	0.0	0.5	0.5	0.0	0.5	0.0	0.0	0.0	0.0	0.0	0.5	2.0
	4															
	T	4.0	9.0	13.0	29.0	3.0	32.0	1.0	13.5	2.5	44.0	38.0	6.0	44.0	67.0	217.0
First Fresh	1	2	15	17	23	6	29	4	17	12	22	31	12	43	58	202
	2	1	4	5	9	3	12	0	8	1	5	0	8	8	14	53
	3	2	4	6	7	0	7	0	5	0	10	0	0	0	6	34
	4															
	T	5	23	28	39	9	48	4	30	13	37	31	20	51	78	289
Sec. Fresh	1	9	6	15	37	0	37	0	2	0	99	45	12	57	78	298
	2	2	2	4	12	0	12	0	2	0	11	0	6	6	11	46
	3	1	0	1	7	0	7	0	1	1	4	0	0	0	4	18
	4															
	T	12	8	20	56	0	56	0	5	1	114	45	18	63	93	352
Fresh Ave.	1	5.5	10.5	16.0	30.0	3.0	33.0	2.0	9.5	6.0	60.5	38.0	12.0	50.0	73.0	250.0
	2	1.5	3.0	4.5	10.5	1.5	12.0	0.0	5.5	0.5	8.0	0.0	7.0	7.0	12.5	50.0
	3	1.5	2.0	3.5	7.0	0.0	7.0	0.0	3.0	0.5	7.0	0.0	0.0	0.0	5.0	26.0
	4															
	T	8.5	15.5	24.0	47.5	4.5	52.0	2.0	18.0	7.0	75.5	38.0	19.0	57.0	90.5	326.0

Male # 11 Group N Replication II

		sag	sb	Total	lag	lb	Total	b	p	ma	mp	i	ie	Total	sg	Total
First Same	1	2	19	21	47	15	62	13	27	5	31	37	24	61	80	300
	2	0	4	4	3	1	4	1	2	0	2	0	0	0	0	13
	3															
	4															
	T	2	23	25	50	16	68	14	29	5	33	37	24	61	80	313
Sec. Same	1	5	2	7	57	7	64	2	2	0	131	68	1	69	105	370
	2	1	2	3	7	0	7	0	1	0	18	0	0	0	3	32
	3															
	4															
	T	6	4	10	64	7	71	2	3	0	149	68	1	69	108	412
Same Ave.	1	3.5	10.5	14.0	52.0	11.0	63.0	7.5	14.5	2.5	81.0	52.5	12.5	65.0	92.5	340.0
	2	0.5	3.0	3.5	5.0	0.5	5.5	0.5	1.5	0.0	10.0	0.0	0.0	0.0	1.5	22.5
	3															
	4															
	T	4.0	13.5	17.5	57.0	11.5	68.5	8.0	16.0	2.5	91.0	52.5	12.5	65.0	94.0	362.5
First Fresh	1	1	34	35	43	27	70	18	57	16	33	43	44	87	95	411
	2	0	20	20	26	5	31	8	21	7	12	0	17	17	21	137
	3	0	16	16	12	3	15	2	14	0	16	0	9	9	13	85
	4	2	11	13	7	2	9	3	9	0	4	0	5	5	5	48
	T	3	81	84	88	37	125	31	101	23	65	43	75	118	134	681
Sec. Fresh	1	1	8	9	73	5	78	0	0	5	183	83	0	83	121	479
	2	6	15	21	29	6	35	3	0	0	18	5	20	25	30	132
	3	0	6	6	9	2	11	2	0	0	9	0	0	0	3	31
	4															
	T	7	29	36	111	13	124	5	0	5	210	88	20	108	154	642
Fresh Ave.	1	1.0	21.0	22.0	58.0	16.0	74.0	9.0	28.5	10.5	108.0	63.0	22.0	85.0	108.0	445.0
	2	3.0	17.5	20.5	27.5	5.5	33.0	5.5	10.5	3.5	15.0	2.5	18.5	21.0	25.5	134.0
	3	0.0	11.0	11.0	10.5	2.5	13.0	2.0	7.0	0.0	12.5	0.0	4.5	4.5	8.0	58.0
	4	1.0	5.5	6.5	3.5	1.0	4.5	1.5	4.5	0.0	2.0	0.0	2.5	2.5	2.5	24.0
	T	5.0	55.0	60.0	99.5	25.0	124.5	18.0	50.5	14.0	137.5	65.5	47.5	113.0	144.0	661.5

Male # 18 Group N Replication II

		sag	sb	Total	lag	lb	Total	b	p	ma	mp	i	ie	Total	sg	Total
First Same	1	1	21	22	3	13	16	0	18	0	33	57	9	66	87	242
	2	2	8	10	2	4	6	0	10	0	10	0	4	4	10	50
	3	0	6	6	1	2	3	0	9	0	16	0	2	2	17	53
	4	0	2	2	0	1	1	0	0	0	0	0	0	0	0	3
	T	3	37	40	6	20	26	0	37	0	59	57	15	72	114	348
Sec. Same	1	2	23	25	13	21	34	0	23	0	49	47	20	67	97	298
	2	0	1	1	0	0	0	2	0	0	0	0	0	0	0	3
	3															
	4															
	T	2	24	26	13	21	34	2	23	0	49	47	20	67	97	301
Same Ave.	1	1.5	22.0	23.5	8.0	17.0	25.0	0.0	20.5	0.0	41.0	52.0	14.5	66.5	92.0	268.5
	2	1.0	4.5	5.5	1.0	2.0	3.0	1.0	5.0	0.0	5.0	0.0	2.0	2.0	5.0	26.5
	3	0.0	3.0	3.0	0.5	1.0	1.5	0.0	4.5	0.0	8.0	0.0	1.0	1.0	8.5	26.5
	4	0.0	1.0	1.0	0.0	0.5	0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.5
	T	2.5	30.5	33.0	9.5	20.5	30.0	1.0	30.0	0.0	54.0	52.0	17.5	69.5	105.5	323.0
First Fresh	1	4	5	9	14	7	21	2	3	10	99	55	0	55	95	294
	2	1	4	5	3	4	7	0	4	6	16	21	12	33	42	113
	3	3	12	15	4	9	13	0	6	0	21	0	15	15	34	104
	4	0	4	4	12	4	16	0	11	0	17	0	1	1	16	65
	T	8	25	33	33	24	57	2	24	16	153	76	28	104	187	576
Sec. Fresh	1	8	21	29	17	22	39	10	7	30	165	75	25	100	155	535
	2	4	11	15	13	26	39	14	11	16	44	2	27	29	39	207
	3	6	29	35	16	26	42	11	35	2	23	0	30	30	35	213
	4	0	19	19	5	4	9	1	20	0	12	0	17	17	30	108
	T	18	80	98	51	78	129	36	73	48	244	77	99	176	259	1063
Fresh Ave.	1	6.0	13.0	19.0	15.5	14.5	30.0	6.0	5.0	20.0	132.0	65.0	12.5	77.5	125.0	414.5
	2	2.5	7.5	10.0	8.0	15.0	23.0	7.0	7.5	11.0	30.0	11.5	19.5	31.0	40.5	160.0
	3	4.5	20.5	25.0	10.0	17.5	27.5	5.5	20.5	1.0	22.0	0.0	22.5	22.5	34.5	158.5
	4	0.0	11.5	11.5	8.5	4.0	12.5	0.5	15.5	0.0	14.5	0.0	9.0	9.0	23.0	86.5
	T	13.0	52.5	65.5	42.0	51.0	93.0	19.0	48.5	32.0	198.5	76.5	63.5	140.0	223.0	819.5

Male # 39 Group N Replication II

		sag	sb	Total	lag	lb	Total	b	p	ma	mp	i	ie	Total	sg	Total
First Same	1	3	13	16	15	10	25	0	6	19	49	45	25	70	107	292
	2	0	3	3	0	0	0	0	1	1	11	0	2	2	13	3
	3	1	1	2	0	0	0	0	2	0	3	0	2	2	3	12
	4	0	1	1	0	0	0	0	0	1	3	0	2	2	4	11
	T	4	18	22	15	10	25	0	9	21	66	45	31	76	127	348
Sec. Same	1	6	36	42	37	13	50	1	16	3	63	49	13	62	109	346
	2	2	16	18	5	6	11	1	3	2	7	0	9	9	19	70
	3	0	4	4	0	0	0	0	2	0	0	0	0	0	1	7
	4															
	T	8	56	64	42	19	61	2	21	5	70	49	22	71	129	423
Same Ave.	1	4.5	24.5	29.0	26.0	11.5	37.5	0.5	11.0	11.0	56.0	47.0	19.0	66.0	108.0	319.0
	2	1.0	9.5	10.5	2.5	3.0	5.5	0.5	2.0	1.5	9.0	0.0	5.5	5.5	16.0	50.5
	3	0.5	2.5	3.0	0.0	0.0	0.0	0.0	2.0	0.0	1.5	0.0	1.0	1.0	2.0	9.5
	4	0.0	0.5	0.5	0.0	0.0	0.0	0.0	0.0	0.5	1.5	0.0	1.0	1.0	2.0	5.5
	T	6.0	37.0	43.0	28.5	14.5	43.0	1.0	5.0	13.0	68.0	47.0	26.5	73.5	128.0	384.5
First Fresh	1	5	25	30	22	13	35	1	23	7	67	48	0	48	107	318
	2	2	40	42	32	11	43	1	32	2	87	21	19	40	123	370
	3	2	4	6	6	1	7	0	3	0	5	0	0	0	2	23
	4															
	T	9	69	78	60	25	85	2	58	9	159	69	19	88	232	711
Sec. Fresh	1	9	18	27	33	7	40	0	0	14	123	107	0	107	184	495
	2	4	16	20	18	12	30	0	0	2	22	53	15	68	85	227
	3	2	4	6	5	4	9	0	0	1	13	0	3	3	14	46
	4	2	3	5	5	2	7	0	0	1	3	0	2	2	6	24
	T	17	41	58	61	25	86	0	0	18	161	160	20	180	289	792
Fresh Ave.	1	7.0	21.5	28.5	27.5	10.0	37.5	0.5	11.5	10.5	95.0	77.5	0.0	77.5	145.5	406.5
	2	3.0	28.0	31.0	25.0	11.5	36.5	0.5	16.0	2.0	54.5	37.0	17.0	54.0	104.0	288.5
	3	2.0	4.0	6.0	5.5	2.5	8.0	0.0	1.5	0.5	9.0	0.0	1.5	1.5	8.0	34.5
	4	1.0	1.5	2.5	2.5	1.0	3.5	0.0	0.0	0.5	1.5	0.0	1.0	1.0	3.0	12.0
	T	13.0	55.0	68.0	60.5	25.0	85.5	1.0	29.0	13.5	160.0	114.5	19.5	134.0	260.5	751.5

Male # 23 Group N Replication III

		sag	sb	Total	lag	lb	Total	b	p	ma	mp	i	ie	Total	sg	Total
First Same	1	3	11	14	43	10	53	3	3	1	46	62	22	84	91	295
	2	1	1	2	7	0	7	0	3	0	3	0	5	5	5	24
	3	1	1	2	1	0	1	1	0	0	0	0	0	0	0	6
	4															
	T	5	13	18	51	10	61	4	5	1	49	62	27	89	96	323
Sec. Same	1	5	16	21	37	6	43	6	10	0	82	83	0	83	107	352
	2	0	3	3	6	0	6	2	2	1	17	0	0	0	5	36
	3															
	4															
	T	5	19	24	43	6	49	8	12	1	99	83	0	83	112	388
Same Ave.	1	4.0	13.5	17.5	40.0	8.0	48.0	4.5	6.5	0.5	64.0	72.5	11.0	83.5	99.0	323.5
	2	0.5	2.0	2.5	6.5	0.0	6.5	1.0	2.0	0.5	10.0	0.0	2.5	2.5	5.0	30.0
	3	0.5	0.5	1.0	0.5	0.0	0.5	0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.0
	4															
	T	5.0	16.0	21.0	47.0	8.0	55.0	6.0	8.5	1.0	74.0	72.5	13.5	86.0	104.0	355.5
First Fresh	1	4	6	10	28	8	36	1	0	0	75	90	1	91	105	318
	2	1	2	3	10	2	12	0	1	1	7	0	7	7	14	45
	3	0	2	2	1	0	1	0	0	2	0	0	0	0	1	6
	4															
	T	5	10	15	39	10	49	1	1	3	82	90	8	98	120	369
Sec. Fresh	1	2	2	4	30	7	37	0	1	1	86	74	0	74	92	295
	2	1	2	3	16	0	16	1	0	2	45	21	0	21	40	128
	3	2	1	3	12	2	14	1	2	0	9	4	11	15	27	71
	4	2	3	5	3	0	3	0	1	0	6	0	2	2	8	25
	T	7	8	15	61	9	70	2	4	3	146	99	13	112	167	519
Fresh Ave.	1	3.0	4.0	7.0	29.0	7.5	36.5	0.5	0.5	0.5	80.5	82.0	0.5	82.5	98.5	306.5
	2	1.0	2.0	3.0	13.0	1.0	14.0	0.5	0.5	1.5	26.0	10.5	3.5	14.0	27.0	86.5
	3	1.0	1.5	2.5	6.5	1.0	7.5	0.5	1.0	1.0	4.5	2.0	5.5	7.5	14.0	38.5
	4	1.0	1.5	2.5	1.5	0.0	1.5	0.0	0.5	0.0	3.0	0.0	1.0	1.0	4.0	12.5
	T	6.0	9.0	15.0	50.0	9.5	59.5	1.5	2.5	3.0	14.0	94.5	10.5	105.0	143.5	444.0

Male # 29 Group N Replication III

		sag	sb	Total	lag	lb	Total	b	p	ma	mp	i	ie	Total	sg	Total
First Same	1	6	19	25	80	9	89	11	26	3	82	46	12	58	117	411
	2	0	2	2	4	0	4	1	3	0	6	0	0	0	3	19
	3															
	4															
	T	6	21	27	84	9	93	12	29	3	88	46	12	58	120	430
Sec. Same	1	1	2	3	72	2	74	1	1	12	109	57	5	62	103	365
	2	1	2	3	18	3	21	0	0	3	21	0	6	6	29	83
	3	0	1	1	5	0	5	0	1	0	7	0	0	0	7	21
	4															
	T	2	5	7	95	5	100	1	2	15	137	57	11	68	139	469
Same Ave.	1	3.5	10.5	14.0	76.0	5.5	81.5	6.0	13.5	7.5	95.5	51.5	8.5	60.0	110.0	388.0
	2	0.5	2.0	2.5	11.0	1.5	12.5	0.5	1.5	1.5	13.5	0.0	3.0	3.0	16.0	51.0
	3	0.0	0.5	0.5	2.5	0.0	2.5	0.0	0.5	0.0	3.5	0.0	0.0	0.0	3.5	10.5
	4															
	T	4.0	13.0	17.0	89.5	7.0	96.5	6.5	15.5	9.0	112.5	51.5	11.5	63.0	129.5	449.5
First Fresh	1	3	22	25	64	15	79	7	10	5	64	49	2	51	85	326
	2	0	4	4	40	6	46	5	3	2	23	0	10	10	31	124
	3	5	6	11	1	0	1	0	0	0	0	0	0	0	1	13
	4															
	T	8	32	40	105	21	126	12	13	7	87	49	12	61	117	463
Sec. Fresh	1	3	5	8	54	3	57	5	2	1	38	63	9	72	91	274
	2	1	4	5	12	2	14	0	0	0	10	0	8	8	16	53
	3	1	1	2	1	0	1	0	0	0	1	0	2	2	3	9
	4	2	0	2	10	0	10	0	0	2	8	0	3	3	11	36
	T	7	10	17	77	5	82	5	2	3	57	63	22	85	121	372
Fresh Ave.	1	3.0	13.5	16.5	59.0	9.0	68.0	6.0	6.0	3.0	51.0	56.0	5.5	61.5	88.0	300.0
	2	0.5	4.0	4.5	26.0	4.0	30.0	2.5	1.5	1.0	16.5	0.0	9.0	9.0	23.5	88.5
	3	3.0	3.5	6.5	1.0	0.0	1.0	0.0	0.0	0.0	0.5	0.0	1.0	1.0	2.0	11.0
	4	1.0	0.0	1.0	5.0	0.0	5.0	0.0	0.0	1.0	4.0	0.0	1.5	1.5	5.5	18.0
	T	7.5	21.0	28.5	91.0	13.0	104.0	8.5	7.5	5.0	72.0	56.0	17.0	73.0	119.0	417.5

Male # 37 Group N Replication III

		sag	sb	Total	lag	lb	Total	b	p	ma	mp	i	ie	Total	sg	Total
First Same	1	1	38	39	13	31	44	18	21	9	106	51	9	60	136	433
	2	0	3	3	0	0	0	4	2	0	5	0	0	0	8	22
	3															
	4															
	T	1	41	42	13	31	44	22	23	9	111	51	9	60	144	455
Sec. Same	1	3	20	23	14	7	21	36	11	4	102	42	0	42	99	338
	2	1	9	10	8	4	12	7	6	1	37	0	12	12	41	126
	3	1	5	6	2	0	2	4	3	1	12	0	0	0	14	42
	4															
	T	5	34	39	24	11	35	47	20	6	151	42	12	54	154	506
Same Ave.	1	2.0	29.0	31.0	13.5	19.0	32.5	27.0	6.0	6.5	104.0	46.5	4.5	51.0	117.5	385.5
	2	0.5	6.0	6.5	4.0	2.0	6.0	5.5	4.0	0.5	21.0	0.0	6.0	6.0	24.5	74.0
	3	0.5	2.5	3.0	1.0	0.0	1.0	2.0	1.5	0.5	6.0	0.0	0.0	0.0	7.0	21.0
	4															
	T	3.0	37.5	40.5	18.5	21.0	39.5	34.5	21.5	7.5	131.0	46.5	10.5	57.0	149.0	480.5
First Fresh	1	7	20	27	13	17	30	6	3	9	79	70	2	72	114	340
	2	0	7	7	8	4	12	0	0	1	16	0	7	7	20	63
	3	0	5	5	8	5	13	0	1	0	17	0	4	4	26	66
	4	2	4	6	5	1	6	3	2	0	10	0	3	3	13	43
	T	9	36	45	34	27	61	9	6	10	122	70	16	86	173	512
Sec. Fresh	1	6	17	23	11	15	26	7	4	0	68	67	5	72	110	310
	2	0	8	8	7	6	13	0	1	2	18	0	10	10	18	70
	3	0	6	6	9	3	12	0	3	0	21	0	7	7	24	73
	4	3	5	8	3	2	5	1	1	0	8	0	4	4	11	38
	T	9	36	45	30	26	56	8	9	2	115	67	26	93	163	491
Fresh Ave.	1	6.5	18.5	25.0	12.0	16.0	28.0	6.5	3.5	4.5	73.5	68.5	3.5	72.0	112.0	325.0
	2	0.0	7.5	7.5	7.5	5.0	12.5	0.0	0.5	1.5	17.0	0.0	8.5	8.5	19.0	66.5
	3	0.0	5.5	5.5	8.5	4.0	12.5	0.0	2.0	0.0	19.0	0.0	5.5	5.5	25.0	69.5
	4	2.5	4.5	7.0	4.0	1.5	5.5	2.0	1.5	0.0	9.0	0.0	3.5	3.5	12.0	40.5
	T	9.0	36.0	45.0	32.0	26.5	58.5	8.5	7.5	6.0	118.5	68.5	21.0	89.5	168.0	501.5

Male # 5 Group CR Replication I

		sag	sb	Total	lag	lb	Total	b	p	ma	mp	i	ie	Total	sg	Total
First Same	1	2	9	11	32	13	45	0	0	0	5	47	19	66	82	209
	2	0	1	1	4	0	4	0	0	0	4	0	3	3	7	19
	3	0	0	0	2	0	2	0	0	0	0	0	1	1	1	4
	4															
	T	2	10	12	38	13	51	0	0	0	9	47	23	70	90	232
Sec. Same	1	Animal not tested due to illness.														
	2															
	3															
	4															
	T															
Same Ave.	1															
	2															
	3															
	4															
	T															
First Fresh	1	15	6	21	58	10	68	0	0	2	115	85	0	85	142	433
	2	0	0	0	7	0	7	0	0	0	1	4	0	4	5	17
	3	1	4	5	14	5	19	0	0	7	7	8	0	8	15	61
	4															
	T	16	10	26	79	15	94	0	0	9	123	97	0	97	162	511
Sec. Fresh	1	Animal not tested due to illness.														
	2															
	3															
	4															
	T															
Fresh Ave.	1															
	2															
	3															
	4															
	T															

Male # 14 Group CR Replication I

		sag	sb	Total	lag	lb	Total	b	p	ma	mp	i	ie	Total	sg	Total
First Same	1	3	10	13	21	9	30	1	7	5	47	65	0	65	87	255
	2	0	2	2	2	1	3	0	0	0	0	0	0	0	1	6
	3															
	4															
	T	3	12	15	23	10	33	1	7	5	47	65	0	65	88	261
Sec. Same	1	2	5	7	21	5	26	0	2	3	35	35	0	35	59	167
	2	1	2	3	3	1	4	0	1	0	8	5	0	5	11	32
	3	3	3	6	2	0	2	0	2	0	12	0	0	0	7	29
	4															
	T	6	10	16	26	6	32	0	5	3	55	40	0	40	77	228
Same Ave.	1	2.5	7.5	10.0	21.0	7.0	28.0	0.5	4.5	4.0	41.0	50.0	0.0	50.0	73.0	211.0
	2	0.0	2.0	2.5	2.5	1.0	3.5	0.0	0.5	0.0	4.0	2.5	0.0	2.5	6.0	19.0
	3	1.5	1.5	3.0	1.0	0.0	1.0	0.0	1.0	0.0	6.0	0.0	0.0	0.0	3.5	14.5
	4															
	T	4.5	11.0	15.5	24.5	8.0	32.5	0.5	6.0	4.0	51.0	52.5	0.0	52.5	82.5	244.5
First Fresh	1	1	11	12	26	13	39	0	4	0	30	41	6	47	78	210
	2	1	9	10	23	7	30	9	10	2	23	2	12	14	30	128
	3	3	19	22	30	26	56	5	10	0	25	15	10	25	35	178
	4	2	1	3	7	2	9	1	3	0	2	0	0	0	1	19
	T	7	40	47	86	48	134	15	27	2	80	58	28	86	144	535
Sec. Fresh	1	2	22	24	33	15	48	1	3	14	35	63	0	63	85	273
	2	4	3	7	26	5	31	1	3	0	21	20	6	26	38	127
	3	0	2	2	8	0	8	0	2	0	4	3	0	3	8	27
	4	0	4	4	13	3	16	0	1	0	15	8	2	10	18	64
	T	6	31	37	80	23	103	2	9	14	75	94	8	102	149	491
Fresh Ave.	1	1.5	16.5	18.0	29.5	14.0	43.5	0.5	3.5	7.0	32.5	52.0	3.0	55.0	82.5	241.5
	2	2.5	6.0	8.5	24.5	6.0	30.5	5.0	6.5	1.0	22.0	11.0	9.0	20.0	34.0	127.5
	3	1.5	10.5	12.0	19.0	13.0	32.0	2.5	6.0	0.0	14.5	9.0	5.0	14.0	21.5	102.5
	4	1.0	2.5	3.5	10.0	2.5	12.5	0.5	2.0	00.0	8.5	4.0	1.0	5.0	9.5	42.5
	T	6.5	35.5	42.0	83.0	35.5	118.5	8.5	18.0	8.0	77.5	76.0	18.0	94.0	147.5	513.0

Male # 16 Group CR Replication I

		sag	sb	Total	lag	lb	Total	b	p	ma	mp	i	ie	Total	sg	Total
First Same	1	10	14	24	20	9	29	0	1	1	62	53	26	79	103	299
	2	1	3	4	2	0	2	0	0	0	7	0	0	0	3	16
	3															
	4															
	T	11	17	28	22	9	31	0	1	1	69	53	26	79	106	315
Sec. Same	1	2	13	15	18	6	24	0	1	3	73	73	16	89	137	342
	2	1	1	2	1	1	2	0	0	0	5	0	0	0	4	13
	3															
	4															
	T	3	14	17	19	7	26	0	1	3	78	73	16	89	141	355
Same Ave.	1	6.0	13.5	19.5	19.0	7.5	26.5	0.0	1.0	2.0	67.5	63.0	23.0	84.0	120.0	320.5
	2	1.0	2.0	3.0	1.5	0.5	2.0	0.0	0.0	0.0	6.0	0.0	0.0	0.0	3.5	14.5
	3															
	4															
	T	7.0	15.5	22.5	20.5	8.0	28.5	0.0	1.0	2.0	73.5	63.0	23.0	84.0	123.5	335.0
First Fresh	1	2	11	13	17	10	27	0	13	2	9	52	19	71	81	216
	2	0	23	23	28	7	35	4	15	10	10	0	34	34	48	179
	3	1	9	10	9	1	10	0	5	0	14	0	16	16	29	84
	4	2	5	7	11	6	17	2	6	3	2	0	11	11	16	64
	T	5	48	53	65	24	89	6	39	15	35	52	80	132	174	543
Sec. Fresh	1	5	21	26	17	7	24	3	11	3	47	68	23	91	111	316
	2	2	29	31	13	7	20	0	12	4	17	0	33	33	45	162
	3	1	8	9	8	2	10	0	12	1	19	0	12	12	24	87
	4	0	8	8	4	0	4	3	1	0	9	0	3	3	8	36
	T	8	66	74	42	16	58	6	36	8	92	68	71	139	188	601
Fresh Ave.	1	3.5	16.0	19.5	17.0	8.5	25.5	1.5	12.0	2.5	28.0	60.0	21.0	81.0	96.0	266.0
	2	1.0	26.0	27.0	20.5	7.0	27.5	2.0	13.5	7.0	13.5	0.0	33.5	33.5	46.5	170.5
	3	1.0	8.5	9.5	8.5	1.5	10.0	0.0	8.5	0.5	16.5	0.0	14.0	14.0	26.5	85.5
	4	1.0	6.5	7.5	7.5	3.0	10.5	2.5	3.5	1.5	5.5	0.0	7.0	7.0	12.0	49.0
	T	6.5	57.0	63.5	53.5	20.0	73.5	6.0	37.5	11.5	63.5	60.0	75.5	135.5	181.0	572.0

Male # 19 Group CR Replication II

		sag	sb	Total	lag	lb	Total	b	p	ma	mp	i	ie	Total	sg	Total
First Same	1	2	27	29	12	18	30	12	40	3	27	24	31	55	79	275
	2	0	7	7	0	1	1	0	14	0	12	0	7	7	14	55
	3	0	3	3	0	0	0	0	0	0	0	0	0	0	0	3
	4															
	T	2	37	39	12	19	31	12	54	3	39	24	38	62	93	333
Sec. Same	1	5	14	19	10	7	17	0	6	2	119	41	10	51	88	302
	2	1	2	3	1	0	1	0	1	0	5	6	4	10	10	30
	3	1	3	4	3	0	3	2	1	0	11	0	0	0	8	29
	4															
	T	7	19	26	14	7	21	2	8	2	135	47	14	61	106	361
Same Ave.	1	3.5	20.5	24.0	11.0	12.5	23.5	6.0	23.0	2.5	73.0	32.5	20.5	53.0	83.5	288.5
	2	0.5	4.5	5.0	0.5	0.5	1.0	0.0	7.5	0.0	8.5	3.0	5.5	8.5	12.0	42.5
	3	0.5	3.0	3.5	1.5	0.0	1.5	1.0	0.5	0.0	5.5	0.0	0.0	0.0	4.0	16.0
	4															
	T	4.5	28.0	32.5	13.0	13.0	26.0	7.0	31.0	2.5	87.0	35.5	26.0	61.5	99.5	347.0
First Fresh	1	2	14	16	9	10	19	0	12	1	72	62	37	99	125	346
	2	3	4	7	2	6	8	0	5	4	24	0	11	11	26	85
	3	1	4	5	0	1	1	0	0	0	1	0	1	1	2	10
	4	1	2	3	2	0	2	0	3	0	8	0	1	1	9	26
	T	7	24	31	13	17	30	0	20	5	105	62	50	112	162	467
Sec. Fresh	1															
	2															
	3															
	4															
	T															
Fresh Ave.	1															
	2															
	3															
	4															
	T															

Animal not tested due to illness.

Male # 21 Group CR Replication II

		sag	sb	Total	lag	lb	Total	b	p	ma	mp	i	ie	Total	sg	Total
First Same	1	4	13	17	9	11	20	0	6	2	17	40	26	66	72	200
	2	0	4	4	0	0	0	0	1	0	1	0	2	2	3	11
	3	0	1	1	0	0	0	0	1	0	1	0	0	0	1	4
	4															
	T	4	18	22	9	11	20	0	8	2	19	40	28	68	76	215
Sec. Same	1															
	2															
	3	Animal not tested due to illness.														
	4															
	T															
Same Ave.	1															
	2															
	3															
	4															
	T															
First Fresh	1	1	22	23	49	35	84	1	54	30	82	34	9	43	128	445
	2	2	13	15	16	18	34	1	11	2	6	7	16	23	32	124
	3	0	6	6	13	5	18	0	11	0	8	0	6	6	12	61
	4	0	3	3	3	2	5	0	1	0	0	0	0	0	0	9
	T	3	44	47	81	60	141	2	77	32	96	41	31	72	172	739
Sec. Fresh	1															
	2															
	3	Animal not tested due to illness.														
	4															
	T															
Fresh Ave.	1															
	2															
	3															
	4															
	T															

Male # 24 Group CR Replication II

		sag	sb	Total	lag	lb	Total	b	p	ma	mp	i	ie	Total	sg	Total
First Same	1	1	6	7	6	9	15	0	13	6	62	61	26	87	100	290
	2	1	4	5	1	2	3	0	0	0	3	1	1	2	4	17
	3	0	1	1	0	1	1	0	2	2	2	0	0	0	3	11
	4															
	T	2	11	13	7	12	19	0	15	8	67	62	27	89	107	318
Sec. Same	1	0	2	2	18	8	26	1	1	26	140	61	7	68	106	370
	2	0	1	1	1	1	2	0	0	3	11	0	0	0	8	25
	3															
	4															
	T	0	3	3	19	9	28	1	1	29	151	61	7	68	114	395
Same Ave.	1	0.5	4.0	4.5	12.0	8.5	20.5	0.5	7.0	16.0	101.0	61.0	16.5	77.5	103.0	330.0
	2	0.5	2.5	3.0	1.0	1.5	2.5	0.0	0.0	1.5	7.0	0.5	0.5	1.0	6.0	21.0
	3	0.0	0.5	0.5	0.0	0.5	0.5	0.0	1.0	1.0	1.0	0.0	0.0	0.0	1.5	5.5
	4															
	T	1.0	7.0	8.0	13.0	10.5	23.5	0.5	8.0	18.5	109.0	61.5	17.0	78.5	110.5	356.5
First Fresh	1	0	26	26	16	26	42	6	35	4	30	45	24	69	101	313
	2	0	7	7	6	8	14	0	5	0	0	0	0	0	0	26
	3															
	4															
	T	0	33	33	22	34	56	6	40	4	30	45	24	69	101	339
Sec. Fresh	1	1	10	11	9	9	18	7	7	9	66	63	2	65	96	279
	2	1	8	9	9	4	13	0	8	0	9	0	5	5	13	57
	3	0	1	1	4	3	7	0	0	0	0	0	0	0	0	8
	4															
	T	2	19	21	22	16	38	7	15	9	75	63	7	70	109	344
Fresh Ave.	1	0.5	18.0	18.5	12.5	17.5	30.0	6.5	21.0	6.5	48.0	54.0	13.0	67.0	98.5	296.0
	2	0.5	7.5	8.0	7.5	6.0	13.5	0.0	6.5	0.0	4.5	0.0	2.5	2.5	6.5	41.5
	3	0.0	0.5	0.5	2.0	1.5	3.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.0
	4															
	T	1.0	26.0	27.0	22.0	25.0	47.0	6.5	27.5	6.5	52.5	54.0	15.5	69.5	105.0	341.5

Male # 30 Group CR Replication III

		sag	sb	Total	lag	lb	Total	b	p	ma	mp	i	ie	Total	sg	Total
First Same	1	5	19	24	95	7	102	3	23	0	159	43	22	65	97	473
	2	1	4	5	5	0	5	3	7	0	6	0	0	0	1	27
	3															
	4															
	T	6	23	29	100	7	107	6	30	0	165	43	22	65	98	500
Sec. Same	1	3	9	12	26	10	36	0	0	0	21	46	17	63	70	202
	2	1	1	2	0	1	1	0	0	0	2	0	0	0	0	5
	3															
	4															
	T	4	10	14	26	11	37	0	0	0	23	46	17	63	70	207
Same Ave.	1	4.0	14.0	18.0	60.5	8.5	69.0	1.5	11.5	0.0	90.0	44.5	19.5	64.0	83.5	337.5
	2	1.0	2.5	3.5	2.5	0.5	3.0	1.5	3.5	0.0	4.0	0.0	0.0	0.0	0.5	16.0
	3															
	4															
	T	5.0	16.5	21.5	63.0	9.0	72.0	3.0	15.0	0.0	94.0	44.5	19.5	54.0	84.0	353.5
First Fresh	1	5	9	14	23	8	31	0	1	0	82	52	4	56	81	265
	2	1	1	2	10	2	12	0	0	0	12	0	4	4	13	43
	3	0	1	1	8	4	12	1	0	0	1	0	3	3	4	22
	4	2	1	3	4	2	6	0	1	1	7	0	3	3	9	30
	T	8	12	20	45	16	61	1	2	1	102	52	14	66	107	360
Sec. Fresh	1	2	9	11	32	8	40	2	6	0	58	50	0	50	69	236
	2	1	5	6	11	88	19	0	4	1	8	7	3	10	14	62
	3	3	7	10	2	7	9	1	2	0	0	0	0	0	0	22
	4															
	T	6	21	27	45	23	68	3	12	1	66	57	3	60	83	320
Fresh Ave.	1	3.5	9.0	12.5	27.5	8.0	35.5	1.0	3.5	0.0	70.0	51.0	2.0	53.0	75.0	250.5
	2	1.0	3.0	4.0	10.5	5.0	15.5	0.0	2.0	0.5	10.0	3.5	3.5	7.0	13.5	52.5
	3	1.5	4.0	5.5	5.0	5.5	10.5	1.0	1.0	0.0	0.5	0.0	1.5	1.5	2.0	22.0
	4	1.0	0.5	1.5	2.0	1.0	3.0	0.0	0.5	0.5	3.5	0.0	1.5	1.5	4.5	15.0
	T	7.0	16.5	23.5	45.0	19.5	64.5	2.0	7.0	1.0	84.0	54.5	8.5	63.0	95.0	340.0

Male # 34 Group CR Replication III

		sag	sb	Total	lag	lb	Total	b	p	ma	mp	i	ie	Total	sg	Total
First Same	1	1	12	13	15	12	27	0	2	11	54	90	24	114	124	345
	2	1	4	5	0	0	0	0	0	0	6	0	0	0	5	16
	3															
	4															
	T	2	16	18	15	12	27	0	2	11	60	90	24	114	129	361
Sec. Same	1	5	25	30	20	11	31	7	9	1	55	34	36	70	77	344
	2															
	3															
	4															
	T	5	25	30	20	11	31	71	9	1	55	34	36	70	77	344
Same Ave.	1	3.0	18.5	21.5	17.5	11.5	29.0	35.5	5.5	6.0	54.5	62.0	30.0	92.0	100.5	344.5
	2	0.5	2.0	2.5	0.0	0.0	0.0	0.0	0.0	0.0	3.0	0.0	0.0	0.0	2.5	8.0
	3															
	4															
	T	3.5	20.5	24.0	17.5	11.5	29.0	35.5	5.5	6.0	57.5	62.0	30.0	92.0	103.0	352.5
First Fresh	1	6	41	47	26	32	58	4	28	15	45	35	13	48	78	323
	2	1	18	19	13	9	22	1	11	0	14	0	7	7	24	98
	3	2	5	7	1	3	4	0	5	0	0	0	0	0	1	17
	4															
	T	9	64	73	40	44	84	5	44	15	59	35	20	55	103	438
Sec. Fresh	1	2	13	15	15	7	22	0	0	16	56	80	13	93	105	307
	2	2	2	4	6	3	9	114	0	1	15	0	9	9	14	166
	3	1	3	4	6	1	7	1	0	0	3	0	4	4	7	26
	4	1	1	2	4	2	6	0	0	0	7	0	2	2	6	23
	T	6	16	25	31	13	44	115	0	17	81	80	28	108	132	522
Fresh Ave.	1	4.0	27.0	31.0	20.5	19.5	40.0	2.0	14.0	15.5	50.5	57.5	13.0	70.5	91.5	215.0
	2	1.5	10.0	11.5	9.5	6.0	15.5	57.5	5.5	0.5	14.5	0.0	8.0	8.0	19.0	132.0
	3	1.5	4.0	5.5	3.5	2.0	5.5	0.5	2.5	0.0	1.5	0.0	2.0	2.0	4.0	21.5
	4	0.5	0.5	1.0	2.0	1.0	3.0	0.0	0.0	0.0	3.5	0.0	1.0	1.0	3.0	11.5
	T	7.5	41.5	49.0	35.5	28.5	64.0	60.0	22.0	16.0	70.0	57.5	24.0	81.5	117.5	480.0

Male # 40 Group CR Replication III

		sag	sb	Total	lag	lb	Total	b	p	ma	mp	i	ie	Total	sg	Total
First Same	1	0	8	8	39	11	50	1	1	12	88	64	4	68	74	302
	2	0	1	1	2	0	2	1	0	0	16	0	0	0	4	24
	3															
	4															
	T	0	9	9	41	11	52	2	1	12	104	64	4	68	78	326
Sec. Same	1	3	5	8	31	15	46	1	0	0	34	47	57	104	107	300
	2	1	2	3	1	0	1	0	0	0	5	0	0	0	2	11
	3															
	4															
	T	4	7	11	32	15	47	1	0	0	39	47	57	104	109	311
Same Ave.	1	1.5	6.5	8.0	35.0	13.0	48.0	1.0	0.5	6.0	61.0	55.5	30.5	86.0	90.5	301.0
	2	0.5	1.5	2.0	1.5	0.0	1.5	0.5	0.0	0.0	10.5	0.0	0.0	0.0	3.0	17.5
	3															
	4															
	T	2.0	8.0	10.0	36.5	13.0	49.5	1.5	0.5	6.0	71.5	55.5	30.5	86.0	93.5	318.5
First Fresh	1	7	23	30	52	14	66	17	19	0	25	85	17	102	85	344
	2	1	11	12	16	3	19	17	4	0	20	0	8	8	16	96
	3	0	2	2	0	1	1	0	0	0	0	0	0	0	0	3
	4															
	T	8	36	44	68	18	86	34	23	0	45	85	25	110	101	443
Sec. Fresh	1	6	21	27	43	12	55	15	17	4	34	91	15	106	97	355
	2	2	8	10	14	4	18	13	6	0	27	0	10	10	12	96
	3	0	1	1	0	2	2	5	0	0	3	0	0	0	2	13
	4															
	T	8	30	38	57	18	75	33	23	4	64	91	25	116	111	464
Fresh Ave.	1	6.5	22.0	28.5	47.5	13.0	60.5	16.0	8.0	2.0	29.5	88.0	16.0	104.0	91.0	349.5
	2	1.5	9.5	11.0	15.0	3.5	18.5	15.0	5.0	0.0	23.5	0.0	9.0	9.0	14.0	96.0
	3	0.0	1.5	1.5	0.0	1.5	1.5	2.5	0.0	0.0	1.5	0.0	0.0	0.0	1.0	8.0
	4															
	T	8.0	33.0	41.0	62.5	18.0	80.5	33.5	3.0	2.0	54.5	88.0	25.0	113.0	106.0	453.5

Male # 1 Group C Replication I

		sag	sb	Total	lag	lb	Total	b	p	ma	mp	i	ie	Total	sg	Total
First Same	1	6	20	26	76	4	80	7	1	19	99	101	0	101	100	433
	2	0	0	0	0	0	0	1	0	0	4	0	0	0	2	7
	3															
	4															
	T	6	20	26	76	4	80	8	1	19	103	101	0	101	102	380
Sec. Same	1	0	12	12	26	8	34	13	21	10	62	57	10	67	73	292
	2	0	1	1	0	1	1	0	5	0	2	0	5	5	7	21
	3	1	2	3	0	1	1	0	1	0	0	0	0	0	0	5
	4															
	T	1	15	16	26	10	36	13	27	10	64	57	15	72	80	318
Same Ave.	1	3.0	16.0	19.0	51.0	6.0	57.0	10.0	11.0	14.5	80.5	79.0	5.0	84.0	86.5	362.5
	2	0.0	0.5	0.5	0.0	0.5	0.5	0.5	2.5	0.0	3.0	0.0	2.5	2.5	4.5	14.5
	3	0.5	1.0	1.5	0.0	0.5	0.5	0.0	0.5	0.0	0.0	0.0	0.0	0.0	0.0	2.5
	4															
	T	3.5	17.5	21.0	51.0	7.0	58.0	10.5	14.0	14.5	83.5	79.0	7.5	86.5	91.0	379.0
First Fresh	1	7	7	14	35	7	42	1	10	0	87	140	0	140	113	407
	2	3	9	12	14	5	19	0	4	6	28	14	6	20	31	120
	3	3	3	6	9	4	13	0	5	0	12	1	9	10	21	67
	4	1	7	8	7	9	16	1	5	2	13	0	9	9	17	71
	T	14	26	40	65	25	90	2	24	8	140	155	24	179	182	665
Sec. Fresh	1	3	36	39	79	5	84	46	51	7	256	50	0	50	88	621
	2	1	14	15	11	1	12	1	17	2	9	18	12	30	33	119
	3	1	7	8	5	2	7	2	7	1	11	0	10	10	14	60
	4	0	4	4	5	1	6	0	1	0	4	0	2	2	5	22
	T	5	61	66	100	9	109	49	76	10	280	68	24	92	140	822
Fresh Ave.	1	5.0	21.5	26.5	57.0	6.0	63.0	23.5	30.5	3.5	171.5	95.0	0.0	95.0	100.5	514.0
	2	2.0	11.5	13.5	12.5	3.0	15.5	0.5	10.5	4.0	18.5	16.0	9.0	25.0	32.0	119.5
	3	2.0	5.0	7.0	7.0	3.0	10.0	1.0	6.0	0.5	11.5	0.5	9.5	10.0	17.5	63.5
	4	0.5	5.5	6.0	6.0	5.0	11.0	0.5	3.0	1.0	8.5	0.0	5.5	5.5	11.0	46.5
	T	9.5	43.5	53.0	82.5	17.0	99.5	25.5	50.0	9.0	210.0	111.5	24.0	135.5	161.0	743.5

Male # 3 Group C Replication I

		sag	sb	Total	lag	lb	Total	b	p	ma	mp	i	ie	Total	sg	Total
First Same	1	5	8	13	18	1	19	17	1	8	33	0	0	0	16	107
	2	2	1	3	7	0	7	7	0	9	10	0	0	0	3	39
	3															
	4															
	T	7	9	16	25	1	26	24	1	17	43	0	0	0	19	146
Sec. Same	1	1	7	8	4	7	11	3	4	4	5	0	0	0	5	40
	2	0	6	6	0	3	3	1	2	3	0	0	0	0	1	16
	3															
	4															
	T	1	13	14	4	10	14	4	6	7	5	0	0	0	6	56
Same Ave.	1	3.0	7.5	10.5	11.0	4.0	15.0	10.0	2.5	6.0	19.0	0.0	0.0	0.0	10.5	73.5
	2	1.0	3.5	4.5	3.5	1.5	5.0	4.0	1.0	6.0	5.0	0.0	0.0	0.0	2.0	27.5
	3															
	4															
	T	4.0	11.0	15.0	14.5	5.5	20.0	14.0	3.5	12.0	24.0	0.0	0.0	0.0	12.5	101.0
First Fresh	1	1	5	6	11	1	12	5	4	8	18	0	0	0	9	62
	2	4	2	6	3	0	3	2	0	6	7	0	0	0	6	30
	3															
	4															
	T	5	7	12	14	1	15	7	4	14	25	0	0	0	15	92
Sec. Fresh	1	3	13	16	13	2	15	4	5	2	11	0	0	0	6	59
	2	1	5	6	5	7	12	5	1	3	3	0	0	0	2	32
	3															
	4															
	T	4	18	22	18	9	27	9	6	5	14	0	0	0	8	91
Fresh Ave.	1	2.0	9.0	11.0	12.0	1.5	13.5	4.5	4.5	5.0	14.5	0.0	0.0	0.0	7.5	60.5
	2	2.5	3.5	6.0	4.0	3.5	7.5	3.5	0.5	4.5	5.0	0.0	0.0	0.0	4.0	31.0
	3															
	4															
	T	4.5	12.5	17.0	16.0	5.0	21.0	8.0	5.0	9.5	19.5	0.0	0.0	0.0	11.5	91.5

Male # 7 Group C Replication I

		sag	sb	Total	lag	lb	Total	b	p	ma	mp	i	ie	Total	sg	Total
First Same	1	1	9	10	8	11	19	8	24	2	77	1	0	1	54	195
	2	0	6	6	0	1	1	1	1	0	2	0	0	0	2	13
	3															
	4															
	T	1	15	16	8	12	20	9	25	2	79	1	0	1	56	208
Sec. Same	1	1	4	5	4	4	8	1	2	4	27	0	0	0	11	58
	2	0	4	4	3	1	4	2	2	1	7	0	0	0	2	22
	3															
	4															
	T	1	8	9	7	5	12	3	4	5	34	0	0	0	13	80
Same Ave.	1	1.0	6.5	7.5	6.0	7.5	13.5	4.5	13.0	3.0	52.0	0.5	0.0	0.5	32.5	126.5
	2	0.0	5.0	5.0	1.5	1.0	2.5	1.5	1.5	0.5	4.5	0.0	0.0	0.0	2.0	17.5
	3															
	4															
	T	1.0	11.5	12.5	7.5	8.5	16.0	6.0	14.5	3.5	56.5	0.5	0.0	0.5	34.5	144.0
First Fresh	1	8	18	26	24	6	30	5	9	2	75	8	0	8	59	214
	2	1	9	10	4	4	8	2	3	0	3	2	1	3	9	38
	3	2	5	7	5	1	6	1	1	0	4	0	0	0	4	23
	4															
	T	11	32	43	33	11	44	8	13	2	82	10	1	11	72	275
Sec. Fresh	1	3	7	10	2	2	4	1	3	0	0	0	0	0	0	18
	2	1	6	7	6	4	10	0	7	0	9	0	0	0	8	41
	3															
	4															
	T	4	13	17	8	6	14	1	10	0	9	0	0	0	8	59
Fresh Ave.	1	5.5	12.5	18.0	13.0	4.0	17.0	3.0	6.0	1.0	37.5	4.0	0.0	4.0	33.5	116.0
	2	1.0	7.5	8.5	5.0	4.0	9.0	1.0	5.0	0.0	6.0	1.0	0.5	1.5	8.5	39.5
	3	1.0	2.5	3.5	2.5	0.5	3.0	0.5	0.5	0.0	2.0	0.0	0.0	0.0	2.0	11.5
	4															
	T	7.5	22.5	30.0	20.5	8.5	29.0	4.5	11.5	1.0	45.5	5.0	0.5	5.5	44.0	167.0

Male # 8 Group C Replication II

		sag	sb	Total	lag	lb	Total	b	p	ma	mp	i	ie	Total	sg	Total
First Same	1	0	6	6	5	0	5	6	4	0	11	0	0	0	7	39
	2	1	3	4	2	1	3	0	1	0	9	0	0	0	10	27
	3															
	4															
	T	1	9	10	7	1	8	6	5	0	20	0	0	0	17	66
Sec. Same	1	3	14	17	8	5	13	0	3	0	7	0	0	0	4	44
	2	1	2	3	8	0	8	4	0	4	17	0	0	0	5	41
	3															
	4															
	T	4	16	20	16	5	21	4	3	4	24	0	0	0	9	85
Same Ave.	1	1.5	10.0	11.5	6.5	2.5	9.0	3.0	3.5	0.0	9.0	0.0	0.0	0.0	5.5	41.5
	2	1.0	2.5	3.5	5.0	0.5	5.5	2.0	0.5	2.0	13.0	0.0	0.0	0.0	7.5	34.0
	3															
	4															
	T	2.5	12.5	15.0	11.5	3.0	14.5	5.0	4.0	2.0	22.0	0.0	0.0	0.0	13.0	75.5
First Fresh	1	2	3	5	12	3	15	7	6	12	49	0	0	0	20	114
	2	4	2	6	7	0	7	1	0	1	11	0	0	0	5	31
	3															
	4															
	T	6	5	11	19	3	22	8	6	13	60	0	0	0	25	145
Sec. Fresh	1	4	8	12	3	1	4	0	0	0	14	0	0	0	6	36
	2	2	4	6	5	2	7	0	0	0	7	0	0	0	2	22
	3															
	4															
	T	6	12	18	8	3	11	0	0	0	21	0	0	0	8	58
Fresh Ave.	1	3.0	5.5	8.5	7.5	2.0	9.5	3.5	3.0	6.0	31.5	0.0	0.0	0.0	13.0	75.0
	2	3.0	3.0	6.0	6.0	1.0	7.0	0.5	0.0	0.5	9.0	0.0	0.0	0.0	3.5	26.5
	3															
	4															
	T	6.0	8.5	14.5	13.5	3.0	16.5	4.0	3.0	6.5	40.5	0.0	0.0	0.0	16.5	101.5

Male # 9 Group C Replication II

		sag	sb	Total	lag	lb	Total	b	p	ma	mp	i	ie	Total	sg	Total
First Same	1	5	13	18	13	6	19	4	12	5	93	9	0	9	72	232
	2	2	3	5	0	0	0	1	5	4	58	11	0	11	57	141
	3	1	3	4	2	0	2	5	4	1	27	0	0	0	22	65
	4															
	T	8	19	27	15	6	21	10	21	10	178	20	0	20	151	438
Sec. Same	1	0	10	10	8	3	11	3	12	2	42	0	0	0	35	107
	2	0	7	7	1	2	3	4	1	1	13	0	0	0	9	38
	3															
	4															
	T	0	17	17	9	5	14	7	13	3	55	0	0	0	44	153
Same Ave.	1	2.5	11.5	14.0	10.5	4.5	15.0	3.5	12.0	3.5	67.5	4.5	0.0	4.5	53.5	173.5
	2	1.0	5.0	6.0	0.5	1.0	1.5	2.5	3.0	2.5	35.5	5.5	0.0	5.5	33.0	89.5
	3	0.5	1.5	2.0	0.0	0.0	1.0	2.5	2.0	0.5	13.5	0.0	0.0	0.0	11.0	32.5
	4															
	T	4.0	18.0	22.0	11.0	5.5	17.5	8.5	17.0	6.5	116.5	10.0	0.0	10.0	97.5	295.5
First Fresh	1	3	11	14	6	7	13	2	4	2	4	0	0	0	6	45
	2	4	5	9	2	4	6	0	1	0	15	0	0	0	14	45
	3															
	4															
	T	7	16	23	8	11	19	2	5	2	19	0	0	0	20	90
Sec. Fresh	1	2	9	11	3	7	10	1	6	1	2	0	0	0	2	33
	2	2	9	11	2	2	4	4	6	1	11	0	0	0	10	47
	3															
	4															
	T	4	18	22	5	9	14	5	12	2	13	0	0	0	12	80
Fresh Ave.	1	2.5	10.0	12.5	4.5	7.0	11.5	1.5	5.0	1.5	3.0	0.0	0.0	0.0	4.0	39.0
	2	3.0	7.0	10.0	2.0	3.0	5.0	2.0	3.5	0.5	13.0	0.0	0.0	0.0	12.0	46.0
	3															
	4															
	T	5.5	17.0	22.5	6.5	10.0	16.5	3.5	8.5	2.0	16.0	0.0	0.0	0.0	16.0	85.0

Male # 10 Group C Replication II

		sag	sb	Total	lag	lb	Total	b	p	ma	mp	i	ie	Total	sg	Total
First Same	1	2	14	16	2	4	6	1	6	2	1	0	0	0	4	36
	2	2	9	11	7	1	8	19	15	2	45	0	0	0	28	128
	3															
	4															
	T	4	23	27	9	5	14	20	21	4	46	0	0	0	32	164
Sec. Same	1	0	3	3	5	2	7	211	0	2	1	0	0	0	2	226
	2	0	1	1	1	1	2	165	1	1	4	0	0	0	2	176
	3															
	4															
	T	0	4	4	6	3	9	376	1	3	5	0	0	0	4	402
Same Ave.	1	1.0	8.5	9.5	3.5	3.0	6.5	106.0	3.0	2.0	1.0	0.0	0.0	0.0	3.0	131.0
	2	1.0	5.0	6.0	4.0	1.0	5.0	92.0	8.0	1.5	24.5	0.0	0.0	0.0	15.0	152.0
	3															
	4															
	T	2.0	13.5	15.5	7.5	4.0	11.5	198.0	11.0	3.5	25.5	0.0	0.0	0.0	18.0	283.0
First Fresh	1	2	7	9	7	3	10	0	2	2	5	0	0	0	8	36
	2	1	4	5	3	1	4	0	12	1	14	2	0	2	15	43
	3	1	3	4	6	2	8	0	1	1	26	0	0	0	22	62
	4															
	T	4	14	18	16	6	22	0	5	4	45	2	0	2	45	141
Sec. Fresh	1	3	9	12	2	3	5	0	2	0	1	0	0	0	1	21
	2	6	9	15	5	3	8	2	2	2	8	0	0	0	7	44
	3															
	4															
	T	9	18	27	7	6	13	2	4	2	9	0	0	0	8	65
Fresh Ave.	1	2.5	8.0	10.5	4.5	3.0	7.5	0.0	2.0	1.0	3.0	0.0	0.0	0.0	4.5	28.5
	2	3.5	6.5	10.0	4.0	2.0	6.0	1.0	2.0	1.5	11.0	1.0	0.0	1.0	11.0	43.5
	3	0.5	1.5	2.0	3.0	1.5	4.0	0.0	0.5	0.5	13.0	0.0	0.0	0.0	11.0	31.0
	4															
	T	6.5	16.0	22.5	11.5	6.5	17.5	1.0	4.5	3.0	27.0	1.0	0.0	1.0	26.5	103.0

Male # 2 Group C Replication III

		sag	sb	Total	lag	lb	Total	b	p	ma	mp	i	ie	Total	sg	Total
First Same	1	1	26	27	31	4	35	2	11	1	18	107	0	107	110	311
	2	0	3	3	0	0	0	0	1	0	0	0	0	0	0	4
	3															
	4															
	T	1	29	30	31	4	35	2	12	1	18	107	0	107	110	315
Sec. Same	1	4	5	9	3	4	7	0	0	0	4	0	0	0	5	25
	2	1	4	5	5	2	7	6	2	4	41	51	0	51	52	168
	3	0	2	2	15	1	16	13	1	5	40	96	0	96	102	275
	4	0	1	1	1	1	2	0	0	1	3	15	0	15	16	38
	T	5	12	17	24	8	32	19	3	10	88	162	0	162	175	506
Same Ave.	1	2.5	15.5	18.0	17.0	4.0	21.0	1.0	5.5	0.5	11.0	53.5	0.0	53.5	57.5	168.0
	2	0.5	3.5	4.0	2.5	1.0	3.5	3.0	1.5	2.0	20.5	25.5	0.0	25.5	26.0	86.0
	3	0.0	1.0	1.0	7.5	0.5	8.0	6.5	0.5	2.5	20.0	48.0	0.0	48.0	51.0	137.5
	4	0.0	0.5	0.5	0.5	0.5	1.0	0.0	0.0	0.5	1.5	7.5	0.0	7.5	8.0	19.0
	T	3.0	20.5	23.5	27.5	6.0	33.5	10.5	7.5	5.5	53.0	134.5	0.0	134.5	142.5	410.5
First Fresh	1	1	5	6	2	5	7	0	0	0	0	0	0	0	0	13
	2	2	4	6	1	0	1	0	0	0	0	0	0	0	0	7
	3															
	4															
	T	3	9	12	3	5	8	0	0	0	0	0	0	0	0	20
Sec. Fresh	1	3	10	13	8	6	14	0	1	1	1	0	0	0	1	31
	2	3	11	14	8	5	13	0	2	3	0	2	0	2	4	37
	3	2	4	6	20	3	23	2	2	0	19	16	0	16	27	95
	4	1	5	6	12	2	14	0	2	1	8	7	0	7	13	51
	T	9	30	39	48	16	64	2	7	5	28	25	0	25	45	214
Fresh Ave.	1	2.0	7.5	9.5	5.0	5.5	10.5	0.0	0.5	0.5	0.5	0.0	0.0	0.0	0.5	22.0
	2	2.5	7.5	10.0	4.5	2.5	7.0	0.0	1.0	1.5	0.0	1.0	0.0	1.0	2.0	22.0
	3	1.0	2.0	3.0	10.0	1.5	11.5	1.0	1.0	0.0	9.5	8.0	0.0	8.0	13.5	47.5
	4	0.5	2.5	3.0	6.0	1.0	7.0	0.0	1.0	0.5	4.0	3.5	0.0	3.5	6.5	25.5
	T	6.0	19.5	25.5	25.5	10.5	36.0	1.0	3.5	2.5	14.0	12.5	0.0	12.5	22.5	117.0

Male # 6 Group C Replication III

		sag	sb	Total	lag	lb	Total	b	p	ma	mp	i	ie	Total	sg	Total
First Same	1	2	8	10	1	4	5	0	1	0	0	0	0	0	0	16
	2	2	2	4	0	0	0	0	0	0	0	0	0	0	0	4
	3															
	4															
	T	4	10	14	1	4	5	0	1	0	0	0	0	0	0	20
Sec. Same	1	2	10	12	4	6	10	0	3	0	2	0	0	0	1	28
	2	1	4	5	1	0	1	0	0	0	1	0	0	0	1	8
	3															
	4															
	T	3	14	17	5	6	11	0	3	0	3	0	0	0	2	36
Same Ave.	1	2.0	9.0	11.0	2.5	5.0	7.5	0.0	2.0	0.0	1.0	0.0	0.0	0.0	0.5	22.0
	2	1.5	3.0	4.5	0.5	0.0	0.5	0.0	0.0	0.0	0.5	0.0	0.0	0.0	0.5	6.0
	3															
	4															
	T	3.5	12.0	15.5	3.0	5.0	8.0	0.0	2.0	0.0	1.5	0.0	0.0	0.0	1.0	28.0
First Fresh	1	3	7	10	0	0	0	0	1	0	4	0	0	0	1	16
	2	1	6	7	4	3	7	0	0	2	14	0	0	0	5	35
	3															
	4															
	T	4	13	17	4	3	7	0	1	2	14	0	0	0	6	51
Sec. Fresh	1	3	9	12	6	6	12	0	0	0	1	0	0	0	0	25
	2	1	5	6	7	1	8	0	2	0	15	0	0	0	2	33
	3															
	4															
	T	4	14	18	13	7	20	0	2	0	16	0	0	0	2	58
Fresh Ave.	1	3.0	8.0	11.0	3.0	3.0	6.0	0.0	0.5	0.0	2.5	0.0	0.0	0.0	0.5	20.5
	2	1.0	5.5	6.5	5.5	2.0	7.5	0.0	1.0	1.0	14.5	0.0	0.0	0.0	3.5	34.0
	3															
	4															
	T	4.0	12.5	17.5	8.5	5.0	13.5	0.0	1.5	1.0	17.0	0.0	0.0	0.0	4.0	54.5

Male # 28 Group C Replication III

		sag	sb	Total	lag	lb	Total	b	p	ma	mp	i	ie	Total	sg	Total
First Same	1	6	12	18	5	10	15	2	1	2	46	0	0	0	12	96
	2	2	5	7	3	3	6	0	0	0	14	0	0	0	10	37
	3															
	4															
	T	8	17	25	8	13	21	2	1	2	60	0	0	0	22	133
Sec. Same	1	1	11	12	1	8	9	0	3	0	0	0	0	0	0	24
	2	1	8	9	2	2	4	1	1	0	1	0	0	0	2	18
	3															
	4															
	T	2	19	21	3	10	13	1	4	0	1	0	0	0	2	42
Same Ave.	1	3.5	11.5	15.0	3.0	9.0	12.0	1.0	2.0	1.0	23.0	0.0	0.0	0.0	6.0	60.0
	2	1.5	6.5	8.0	2.5	2.5	5.0	0.5	0.5	0.0	7.5	0.0	0.0	0.0	6.0	27.5
	3															
	4															
	T	5.0	18.0	23.0	5.5	11.5	17.0	1.5	2.5	1.0	30.5	0.0	0.0	0.0	12.0	87.5
First Fresh	1	8	19	27	13	11	24	1	3	0	29	0	0	0	22	106
	2	1	10	11	6	2	8	1	2	0	13	0	0	0	10	45
	3															
	4															
	T	9	29	38	19	13	32	2	5	0	42	0	0	0	32	151
Sec. Fresh	1	7	22	29	6	13	19	2	4	0	10	0	0	0	11	75
	2	2	12	14	9	5	14	0	3	0	13	0	0	0	8	52
	3															
	4															
	T	9	34	43	15	18	33	2	7	0	23	0	0	0	19	127
Fresh Ave.	1	7.5	20.5	28.0	9.5	12.0	21.5	1.5	3.5	0.0	19.5	0.0	0.0	0.0	16.5	90.5
	2	1.5	11.0	12.5	7.5	3.5	11.0	0.5	2.5	0.0	13.0	0.0	0.0	0.0	9.0	48.5
	3															
	4															
	T	9.0	32.5	40.5	17.0	15.5	32.5	2.0	6.0	0.0	32.5	0.0	0.0	0.0	25.5	139.0

BIOGRAPHICAL SKETCH

Carol K. Flesher was born May 28, 1931, in Salem, Oregon, where she attended public schools, graduating from Salem Senior High School in 1950. She entered St. Petersburg Junior College in 1955 and took an Associate of Arts degree in 1957. Her undergraduate training was completed at the University of Florida where she received a B.A. with honors in 1959 and a M.A. degree in 1960. At that time she entered doctoral training at the University of Florida, completing the requirements for the Ph.D. degree in the summer of 1964. Her undergraduate and M.A. training was accomplished under a scholarship awarded by the Veteran's Administration. During the period 1960 to 1961, she received a special research assistantship fellowship from the Association of Landgrant Colleges. From 1961 through 1964 she held a U. S. Public Health predoctoral research fellowship.

Carol K. Flesher is a member of Phi Theta Kappa, Phi Beta Kappa, and Phi Kappa Phi.

This dissertation was prepared under the direction of the chairman of the candidate's supervisory committee and has been approved by all members of that committee. It was submitted to the Dean of the College of Arts and Sciences and to the Graduate Council, and was approved as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

August 8, 1964

E. Ruffin Jones

Dean, College of Arts and Sciences

Dean, Graduate School

Supervisory Committee: